PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON
Session 1954–55

Vol. 167 Part 2

PROCEEDINGS OF THE GENERAL MEETING HELD ON 3 February 1955

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 20 January 1955, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. H. H. Bloomer, Mrs. Joan Eyles, Mr. P. Greig-Smith, Dr. Isabella Gordon, Mr. F. N. Howes, Mr. E. E. Sherff, the Trustees of the British Museum and Dr. C. R. Metcalfe.

The PRESIDENT reported the death of the Rev. Arthur George Gregor, M.A., B.D., Fellow.

The following communication was read and discussed :—

Mr. J. W. S. PRINGLE, M.B.E., F.R.S. The Evolution of Cicada Song. (Discussed by Dr. E. B. Worthington, Dr. W. E. China, Dr. S. M. Manton, Mr. D. W. Tucker, Dr. G. S. Carter, Dr. B. P. Uvarov, Mr. E. J. H. Corner, the President and Dr. L. Harrison Matthews; Mr. Pringle replied.) **[Printed in full on p. 144.]**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 17 February 1955

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 3 February 1955, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. W. G. Mackenzie, Col. F. C. Stern, O.B.E., M.C. and Imperial Chemical Industries Ltd.

Mr. Philip Arthur Richard Street, M.Sc. signed the Obligation in the Roll and Charter Book and was admitted a Fellow.

The PRESIDENT reminded Fellows that proposals for Officers and New Members of Council under Bye-Law, Chap. 8, Sect. 2, and for Foreign Members and Associates *honoris causa*, should be forwarded to the General Secretary not later than 4 April 1955.

The following communications were read and discussed :—

Professor IRENE MANTON. Flagella structure based on observations with the electron microscope.

Abstract,—

Evidence of the external and internal structure of cilia in the Plant Kingdom was shown.

Dr. J. R. G. BRADFIELD. Fibre patterns in animal cilia and flagella.

Abstract,—

Cilia and flagella from a variety of animals have recently been shown to contain 11 straight longitudinal fibres—a cylinder of 9 equal outer fibres surrounding 2 central fibres. The only genuine divergence from this " 9+2 " pattern which has so far been encountered is in the mammalian sperm tail, where there is an additional cylinder of 9 fibres, giving a " 9+9+2 " pattern. Of the 9 *outer* fibres in the mammalian sperm tail, 3 are distinctly thicker than the other 6 ; but all 9 *outer* fibres are much thicker than the *inner* 9 fibres.

In the light of the extensive experimental work which has been done on cilia and flagella it is not difficult to make hypotheses regarding the ways in which these fibre-arrays might produce the movements observed. But there is no experimental evidence at the electron microscope level which would permit verification or rejection of such hypotheses. Nor does it at present seem possible to suggest convincing explanations, either mechanical or morphogenetic, for the mysterious constancy of the 9+2 motif.

(The communications were discussed by Dr. G. S. Carter, Dr. R. Melville, Mr. R. Ross, Dr. E. M. Delf and the Zoological Secretary ; Prof. Manton and Dr. Bradfield replied.)

PROCEEDINGS OF THE GENERAL MEETING HELD ON 3 March 1955

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 17 February 1955, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. A. E. Blake, K.L.B. and the National Museum of Wales.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Miss Joan E. Heriot, M.Sc., Miss Kathleen Mabel Archard, B.Sc. and Miss Ursula K. Smith, B.Sc.

The PRESIDENT reported the deaths of William Charles BARTON and Dr. Thomas JOHNSON, Fellows of the Society.

Certificates of recommendations for election to Fellowship were read for the first time in favour of :—Ronald Goulding Atkinson, B. H. Choudhury, M.Sc., William Grant Inglis, B.Sc., Fred Ronald Jones, B.Sc., Professor R. P. Roy, M.Sc., Ph.D., George Wenham Shaw, M.Sc., A.L.S., T. Sreeramulu, M.Sc., Ernest William Shurly, Thomas Jennings Wallace, T.D., B.Sc. and Colonel Richard William Wren.

The following communications were read and discussed :—

Dr. T. B. REYNOLDSON. Current taxonomy of the freshwater triclads of the British Isles. (Discussed by Dr. E. B. Worthington, Mr. J. B. Gillett, Dr. G. S. Carter, Dr. H. E. Quick, the President, Dr. Edward Hindle, the Botanical Secretary and Mr. E. J. H. Corner ; Dr. Reynoldson replied.)

Abstract,—

Triclad flatworms are found abundantly in most of our streams and lakes yet their taxonomy has been neglected by British zoologists. Eight species were recognized in 1923 and since then five species have been added. The majority are easily distinguished by external features but particular difficulty occurs within the genus *Polycelis*. This and other problems have been resolved to a large extent by cytological studies mainly by Swedish and Italian workers. Polyploidy has been found to occur commonly in the group with consequent parthenogenetic reproduction. The distribution of polyploid types varies from one area to another. The presence of an introduced American species has been recently discovered. Earlier, this had been confused with the externally similar continental species *Dugesia* (=*Planaria*) *subtentaculata*. Recently, the ecology of lake species has been widely studied in this country. The results show a well-defined pattern of distribution, both qualitative and quantitative, in relation to lake type. This was briefly dealt with.

Dr. G. S. Carter. The Papyrus Swamps of Uganda. The Nature of the Environment. (Discussed by Dr. E. B. Worthington, Dr. T. B. Reynoldson, Mr. R. Ross, Dr. E. Trewavas, the Zoological Secretary and Mr. J. B. Gillett; Dr. Carter replied.)

Abstract,—

In Uganda and other parts of Central Africa swamps in which papyrus is dominant cover large areas at the margins of lakes and in shallow valleys, which are often filled with these swamps for many miles. This paper gives the results of a year's work, carried out in the country near Jinja on Lake Victoria, on the biological conditions in the waters of the swamps.

Some description is given of the physiography of the swamps and of the lily zone which lies between the lake swamps and the open water of the lake.

Analyses of the surface water in the lake swamps showed a steep and regular gradient of conditions between the open water of the lake and the shore. De-oxygenation, carbon-dioxide content, acidity, and contents of many chemical constituents increase regularly as the shore is approached. At a distance of 25 yds. within the swamp even the surface water is entirely without oxygen and has a carbon-dioxide content of as much as 40–50 p.p.m. The conditions are still more extreme in the water below the floating mat that the papyrus forms at a foot below the water surface.

In the valley swamps similar conditions were found except where open pools occur among the papyrus.

These findings give a complete explanation of the poverty of the fauna of the swamps, especially the fish fauna. Except in the open pools in the valley swamps, the only fishes to be found are the air-breathing forms, *Clarias* and *Protopterus*.

In both the valley swamps and the parts of the lake swamps near the shore, the water is derived from land water very different in its chemical constitution from the water of the lake. This water becomes de-oxygenated as it flows through the swamp, owing to the conditions of shade, absence of wind disturbance and of overturn at night. In wet weather a stream of this land water flows through the lake swamps, mainly below the mat, and may reach the lily zone, there modifying conditions for the relatively rich fauna.

The question whether it would be possible by any form of treatment to so alter conditions in the valley swamps that they might become suitable for fish farms was considered. [A full report of this paper has been published *"The Papyrus Swamps of Uganda", Heffer, Cambridge*].

PROCEEDINGS OF THE GENERAL MEETING HELD ON 17 March 1955

Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 3 March 1955, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. I. H. Burkill, Dr. T. J. Jenkin, C.B.E., Col. F. C. Stern, O.B.E., M.C., the University of Liverpool and the Metropolitan Water Board.

Mr. Keith B. Carlisle, B.Sc., signed the Obligation in the Roll and Charter Book, and was admitted a Fellow.

The President reported the deaths of Professor Dr. August Adriaan Pulle and Dr. Liberty Hyde Bailey, Foreign Members of the Society.

Certificates of recommendation for election to Fellowship in favour of those candidates whose names were printed in the report of the Meeting held on 3 March 1955 were read for the second time.

Certificates of recommendation for election to ordinary Associateship were read for the first time in favour of :—James Bergin, Miss Margaret Winifred Cornish, M.Sc., George Arthur Nixon and Barné Tod Stern, B.Sc.

The following communications were read and discussed :—

The Freshwater Biological Association, Ambleside. Chemical analysis in ecology illustrated from Lake District tarns and lakes. Mr. F. J. H. Mackereth : Chemical differences. Dr. J. W. G. Lund : Algal differences. Dr. T. T. Macan : Faunistic differences. (Discussed by Dr. G. S. Carter, Dr. E. B. Worthington, Mr. R. Ross, Mr. D. A. Parry, Prof. T. M. Harris, Prof. G. C. Varley and Dr. W. Rushton ; Mr. Mackereth, Dr. Lund and Dr. Macan replied.) **[Printed in full on pp. 159-175.]**

PROCEEDINGS OF THE GENERAL MEETING HELD ON 21 April 1955

Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 17 March 1955, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. J. N. Carreck, Mr. P. R. G. Jackson, Dr. L. M. J. Kramer, Mr. Richard Morse, Mr. A. A. Prestwich, Dr. T. A. Sprague and the Nature Conservancy.

Mr. James Eldred Cuthbert Brokenshire signed the Obligation in the Roll and Charter Book and was admitted a Fellow.

The following were elected Auditors of the Treasurer's Accounts for 1954–55 under Chap. 10, Sect. 7 of the Bye-Laws :—

Representing the Council : Dr. A. TINDELL HOPWOOD,
Dr. C. R. METCALFE.

Representing the Fellows : Mrs. F. L. BALFOUR-BROWNE,
Dr. ERROL I. WHITE.

The PRESIDENT reported the deaths of Rev. Pierre TEILHARD DE CHARDIN, S.J., Foreign Member, William Robert SHERRIN, Associate *honoris causa* and James JACK, Eleanor PEARSE, Henry Augustus Hammond DUNN and Robert Vernon Giffard WOOLEY, Fellows.

Certificates of recommendation for election to membership were read for the first time in favour of the following :—*Foreign Members* :—Dr. Bernard O. Dodge, New York, U.S.A., Professor Elias Melin, Uppsala, Sweden, and Professor William Randolph Taylor, Michigan, U.S.A. *Associate* honoris causa :—Gerald Atkinson. *Fellows* :—Geoffrey Fryer, B.Sc., Professor William Edwyn Isaac, Ph.D., Professor S. B. Kausik, D.Sc., Revd. Rene Lavocat, Peter Harold Lowings, Ph.D., Cyril Winthrop Mackworth-Praed, M.A., Gordon Scurfield, Ph.D. and George Usher, B.Sc.

The following candidates for Fellowship and Ordinary Associateship were balloted for and elected. FELLOWS :—Ronald Goulding Atkinson, B. H. Choudhury, M.Sc., William Grant Inglis, B.Sc., Fred Ronald Jones, B.Sc.. Professor R. P. Roy, M.Sc., Ph.D., George Wenham Shaw, M.Sc., A.L.S., T. Sreeramuli, M.Sc., Ernest William Shurly, Thomas Jennings Wallace, T.D., B.Sc., Colonel Richard William Wren. ORDINARY ASSOCIATES :—James Bergin, Miss Margaret Winifred Cornish, M.Sc., George Arthur Nixon, Barné Tod Stern, B.Sc.

The PRESIDENT announced that the Council had nominated Sir John Graham Kerr, F.R.S. for the Award of the Linnean Gold Medal for 1955.

The following communication was read and discussed :—

Professor J. HESLOP HARRISON. Natural Hybridisation and its Consequences in the British Dactylorchids. (Discussed by Mr. A. H. G. Alston, Dr. R. Melville, Mr. N. Y. Sandwith, Mr. D. C. McClintock, Mr. P. R. Bell, the Zoological Secretary and Mrs. A. N. Gibby ; Professor Harrison replied.) **[Printed in full on pp. 176-185.]**

The following papers were read in title :—

A note on *Brechites penis* (L.). By R. D. PURCHON, F.L.S.

A new genus of *Meliaceae* from Eastern Africa. By BERNARD VERDCOURT, F.L.S.

Some new species of Cyclops sensu lato. (Crustacea : Copepoda) from Nigeria. By S. D. ONABAMIRO, F.L.S.

Notes on Cameroons Commelinas—*Commelina cameroonensis* sp. nov. and *C. mannii* C. B. Clarke, redescribed. By J. K. MORTON. (Communicated by the Botanical Secretary.)

The structure and biology of *Vallicula muliformis* gen. et sp. nov., a platycyctenid ctenophora. By J. RANKIN. (Communicated by Dr. C. F. A. Pantin, F.R.S., F.L.S.)

An essay on Evolution and modern Genetics. By H. Graham Cannon, F.R.S., F.L.S.

Some Locomotory adaptations in Mammals. By J. Maynard Smith and R J. G. Savage, F.L.S.

On the occurrence of secondary thickening in palaeozoic Ferns. By H. S. Holden, F.L.S.

Anthicidae (Coleoptera) of the High Simien district, Northern Ethiopia. By C. N. Hawkins. (Communicated by Hugh Scott, Sc.D., F.R.S., F.L.S.)

Studies in diurnal rhythms V. Nocturnal ecology and water-relations of the British cribellate spiders of the genus *Ciniflo* Bl. By J. L. Cloudsley-Thompson, F.L.S.

Observations on Flying and Flightless Water Beetles. By Dorothy Jackson, F.L.S.

Reports on the Percy Sladen Trust Expedition to Lake Titicaca in 1937:—

Hydrachnellae. By Karl Viets.
Mollusca : Gastropoda. By Fritz Haas.
The Anatomy of the Gastropoda. By Bengt Hubendick.
Crustacea : Cladocera. By J. P. Harding, F.L.S.
Polyzoa. By Eveline du Bois-Reymond Marcus.
Crustacea : Copepoda. By J. P. Harding, F.L.S.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 5 May 1955

Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 21 April 1955, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. R. G. Atkinson, Mrs. W. C. Barton, Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S. and the Imperial Chemical Industries, Ltd.

Colonel Richard William Wren and Mr. T. Sreeramulu signed the Obligation in the Roll and Charter Book and were admitted Fellows.

Certificates of recommendation for election to Fellowship and Foreign Membership were read for the second time in favour of those named in the Proceedings of the General Meeting held on 21 April 1955.

The following communication was read and discussed :—

Dr. C. F. A. Pantin, F.R.S. Terrestrial Nemertines and Convergent Evolution. (Discussed by the President, Dr. S. M. Manton, the Zoological Secretary, Dr. G. S. Carter, the Botanical Secretary and Professor G. C. Varley ; Dr. Pantin replied.)

Abstract,—

The Nemertine worms are characteristically marine animals, but some fourteen terrestrial species have been described. These are all relatively primitive Metanemertines. They possess a curious distribution. They have been found in Australia, New Zealand, and in various islands in the Atlantic and Indo-Pacific Oceans. Some have been introduced into the British Isles, and also into greenhouses in continental Europe. They are not known from the great continents. Their specific characters have not been well described. Notwithstanding older statements, these animals have well developed excretory systems ; which on physiological grounds might be expected. The nephridia and the vascular system in particular, as well as other features, provide good diagnostic characters. When an attempt is made to group the species it is found quite impossible to make a classification which does not imply the independent evolution of more than one diagnostic character. The nature of these evolutionary convergences is of considerable interest. Making allowance for this, three distinct groups of species can be distinguished. Two of these can be related to distinct genera of marine nemertines to be found in certain parts of the world near high water mark (a very common habitat for Nemertines). Thus there is a common and undescribed littoral nemertine in the South Island of New Zealand which shares many characters with the New Zealand and Australian terrestrial species, but differs from all the other terrestrial ones.

PROCEEDINGS OF THE ANNIVERSARY MEETING

24 May 1955

Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., President, in the Chair.

The PRESIDENT welcomed the presence at the Meeting of members of Sir John Graham Kerr's family and expressed the Society's regret that Sir John Graham Kerr was unable to be present.

The Proceedings of the General Meeting held on Thursday, 5 May 1955, were read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Professor J. Omer-Cooper, Colonel F. C. Stern, O.B.E., M.C., Imperial Chemical Industries, Ltd., and the National Museum of Wales, Cardiff.

The following signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Mr. Ernest William Shurly and Mr. Bernard Verdcourt, B.Sc.

Candidates for membership were balloted for and elected :—

Fellows.—Geoffrey Fryer, B.Sc., Professor William Edwyn Isaac, Ph.D., Professor S. B. Kausik, D.Sc., Revd. Réné Lavocat, Peter Harold Lowings, Ph.D., Cyril Winthrop Mackworth-Praed, M.A., Gordon Scurfield, B.Sc., Ph.D. and George Usher, B.Sc.

Foreign Members.—Dr. Bernard Ogilvie Dodge, Professor Elias Melin and Professor William Randolph Taylor.

Associate honoris causa.—GERALD ATKINSON.

The Bye-Laws regulating the Election of Council and Officers having been read by the General Secretary, the President declared the Ballot for new Members of Council to be open, and voting began. The President thereafter appointed Dr. J. K. Spearing, Mr. R. H. Jeffers and Mr. N. Y. Sandwith, as Scrutineers of the Ballot.

The Ballot was closed at the due time, and the result declared to the Meeting.—NEW MEMBERS OF COUNCIL.—Mr. Peter R. Bell, Dr. Margaret E. Brown, Dr. A. J. Cain, Mr. C. C. Hentschel and Dr. H. Hamshaw Thomas, M.B.E., F.R.S.

The retiring Councillors were Mr. J. E. Dandy, Professor P. B. Medawar, F.R.S., Mr. E. Milne-Redhead, Dr. T. C. S. Morrison-Scott, D.S.C. and Dr. W. E. Swinton.

The PRESIDENT declared the Ballot of Officers to be open and voting began. The Ballot was closed at the due time, and the result declared to the Meeting. —OFFICERS.—*President* : Dr. H. HAMSHAW THOMAS, M.B.E., F.R.S. ; *Treasurer* : Colonel F. C. STERN, O.B.E., M.C. ; *Zoological Secretary* : Mr. H. R. HEWER, M.Sc. ; *Botanical Secretary* : Dr. GEORGE TAYLOR.

The Financial Report was given by the Treasurer and the Accounts of the Society, duly audited, for the year 1954–55, were laid before the meeting.

TREASURER'S REPORT

Printed copies of the accounts for the financial year which ended on 30 April 1955, are before you. For comparison, the figures for last year are printed in italics on the left-hand-side. A statement has been prepared by the Auditors who certify as to details; the Audit Committee has inspected the books, verified the investments and bank balances and passed the accounts; the action of the Committee has been confirmed by the Council.

I will briefly go through the accounts and deal with the main items :—

On the Income Side.

The total of Annual Contributions is slightly lower due to less arrears having been received. Many arrears were received in the previous year leaving fewer Annual Contributions outstanding.

It will be seen that we received £283 in refund of *Income Tax on Deeds of Covenants* signed by Fellows. This was less than last year, mainly due to the reduction of sixpence in the standard rate of tax, and the death of some covenantors. It is hoped that the receipts this year will considerably increase as the result of some further one hundred Fellows agreeing to covenant in response to the President's recent letter on the subject of Annual Contributions. These covenants, which do not effect the amount contributed by Fellows, are a great help to the finances of the Society and it is very much hoped that as many Fellows as possible will sign a Deed of Covenant.

It will be noted that *Interest and Dividends* is about £50 less than last year. Last year's figure included Deposit Account interest for two years credited in the one year.

Sales of Publications are not quite so high as last year's record figure, but they are still well above the average receipts. The Society received through the Royal Society the sum of £1,000 from the Parliamentary grant-in-aid for Publications. We are deeply grateful for this help to our funds for expenditure on Publications. We have, however, been informed that we cannot consider this assistance towards the cost of Publications in the nature of an Annual Grant, and that steps should be taken by the Society to improve their financial position. The Council propose to make recommendations when they have had an opportunity of considering the replies to the President's letter on the subject of Annual Contributions and Publications.

The transfer from the Hooker Lecture and Westwood Funds Account is in respect of the cost of printing the Hooker Lecture in the *Proceedings* and the cost of illustrating a paper by H. Womersley, Associate *honoris causa*, appearing in the *Journal Zoology.*

On the Payment Side.

Gas, electricity and Fuel have cost slightly more due to the increase in fuel costs.

Furniture and Repairs are much lower as no major re-decoration has been necessary.

I should like to say a word now with regard to the *finance* of *Publications* which is such an important aspect of the work of the Society.

It will be noticed that the amount spent on publications this year has been £1,204 against £1,366 in the previous year.

During the Session 1954–55, one *Journal Zoology*, two *Journals Botany*, one part of the *Proceedings* and one *Synopsis* were issued.

A further part of the *Proceedings*, which has been paid for, is waiting distribution by the *Printers*.

In the press now, or passed for publication, is sufficient material for four *Journals Zoology*, two *Journals Botany* and two parts of the *Proceedings*, so that the figure for publications this coming year will be very much higher than for the past two years and will necessitate drawing upon the Publications Reserve now standing at £3,990. The sum of £1,100 from the balance in hand this year, which would have been expended on publications during the year except for the delays in printing, is included in the above amount. The Society is making strong representations to its Printers in an endeavour to speed up the issue of the Society's publications.

Printing costs have remained fairly stationary this past year, but the Society has been notified of a General Increase of 10% as from 1 May 1955.

Library Account transfer. The allocation from the General Account has been increased from £300 to £500 to meet the continued rise in the cost of the Library.

Salaries and Wages. This figure is higher than last year due mainly to the necessity of employing additional assistance in the Library because of the Librarian's long illness.

THE LIBRARY ACCOUNT

The Account has a balance of £91 after paying the usual items. The cost of binding is a heavy burden and the Library Committee are considering ways and means of reducing the amount of binding which is necessary.

THE LIBRARY RESTORATION FUND

This Fund now has only a balance of £723 out of £3,440 subscribed up to date. The binding and repairs of books and periodicals has amounted to about £1,567; the purchase of war-issues of foreign works missing from our sets cost £374, additional shelving for the Library Annexe £610 and £183 for a new carpet for the Library.

Although a great deal of binding, which is becoming increasingly expensive, and the buying of foreign books has been done, more is still needed. The important work of repairing the unique books of Linnaeus's Library is to be carried out this year by a first class firm at a cost of some £300.

The Society has received only £19 towards this fund this last year. I should like again to make a particular appeal to all friends of the Linnean Library to help this Fund in any way they can by donations or by legacies, in order that this historic and valuable Library can be maintained and conserved, as it should be.

FELLOWS' POSTAL ACCOUNT

It will be seen that for the first time for many years transactions have taken place in this account. In view of the large increase in parcel post rates the Council found it necessary to ask Fellows to refund postage on the books sent on loan.

TREASURER'S ACCOUNTS FOR THE
(Presented at the Anniversary
Receipts and Payments of the Linnean Society

General

1953–54 £	RECEIPTS	£	s.	d.	1954–55 £	s.	d.
	To Balance at 1 May 1954 :—						
	Current Account at Bank	254	16	9			
	Deposit Account at Bank	100	0	0			
	Deposit Account Post Office Savings Bank	436	16	8			
	Cash in hand	15	7	11			
695					807	1	4
76	,, Admission Fees				60	0	0
	,, Arrears of Annual Contributions	40	0	0			
	,, Annual Contributions for year	2743	0	0			
	,, in advance	95	12	3			
2988					2878	12	3
28	,, of Associates				17	0	0
348	,, Income Tax recovered on Deeds of Covenant				283	7	10
81	,, Composition Fees				44	0	0
424	,, Interest and Dividends (including Income Tax recovered)				372	7	5
116	Post Office Savings Bank Account				119	3	0
	,, Sales of Publications :—						
	Transactions	64	1	9			
	Journals	546	11	6			
	Proceedings &c.	275	10	7			
978					886	3	10
	,, Grants in aid of Publications :—						
950	Royal Society	1000	0	0			
	Mr. H. Womersly	20	0	0			
15	*Prof. J. McLean Thompson*	——					
25	*Mr. J. D. Snowden*	——					
					1020	0	0
127	,, Miscellaneous Receipts				167	12	10
—	,, Transfers from Trust Funds :—						
	Hooker Lecture Fund	90	10	1			
	Westwood Fund	88	16	0			
					179	6	1
£6851					£6834	14	7

Library

£		£	s.	d.	£	s.	d.
199	To Balance at 1 May 1954				174	13	3
79	,, Interest on Investments (including Income Tax recovered)				78	17	3
10	,, Donations : John Innes Horticultural Institution	10	0	0			
	Imperial Chemical Industries Ltd.	21	0	0			
					31	0	0
300	,, Transfer from General Account				500	0	0
—	,, Transfer from Library Restoration Fund				200	0	0
100	,, *Gift in Memory of Miss Maud Williams*				——		
58	,, *War Damage Settlement on F. Druce Bequest*				——		
£746					£984	10	6

Library

£		£	s.	d.
870	To Balance at 1 May 1954	903	6	9
18	,, Donations : Fellows and Friends	19	6	0
15	,, Interest on Deposit Account		8	11
£903		£923	1	8

Fellows' Postal

£		£	s.	d.
50	To Balance at 1 May 1954	50	6	5
—	,, Deposit	1	0	0
£50		£51	6	5

YEAR ENDED 30 APRIL 1955

Meeting, 24 May 1955)

from 1 *May* 1954 *to* 30 *April* 1955

Account

1953–54 £	PAYMENTS	£	s.	d.	1954–55 £	s.	d.
227	By Electricity, Gas and Fuel				239	3	6
469	,, Furniture and Repairs				79	6	0
91	,, National Insurance and Fire Insurance				88	18	8
320	,, Miscellaneous Printing and Stationery and Dispatch				275	19	3
428	,, Petty Expenses and Postages				398	15	8
	,, Publications :—						
	Printing	810	0	9			
	Distribution	106	5	3			
	Illustrations	288	6	7			
1366					1204	12	7
900	,, Transfer to Reserve for Publications Fund	1100	0	0			
300	,, Transfer to Library Account	500	0	0			
					1600	0	0
1645	,, Salaries, Wages and Pension				1795	18	7
15	,, Donations : Zoological Record (Vol. 90)	15	0	0			
—	International Union for Nature Protection	2	2	0			
—					17	2	0
—	,, International Assoc. for Plant Taxonomy—Subscription				3	10	0
108	,, Staff Annuities (Annual Premiums)				108	0	0
144	,, Investment of Compounders' Fees				185	0	0
31	,, Linnean Medal				27	13	4
	,, Balance at 30 April 1955 :—						
	Current Account at Bank	58	18	5			
	Deposit Account at Bank	650	0	0			
	Deposit Account Post Office Savings Bank	87	5	0			
	Cash in hand	14	11	7			
807					810	15	0
	Note :—Balance of Composition Fees to be invested is £44.						
£6851					£6834	14	7

Account

£		£	s.	d
212	By Periodicals	266	14	8
252	,, Binding	524	12	3
108	,, Books	102	0	1
	,, Balance at 30 April 1955 :—			
174	Current Account	91	3	6
£746		£984	10	6

Restoration Fund

£		£	s.	d.	£	s.	d.
–	By Transfer to Library Account				200	0	0
	,, Balance at 30 April 1955 :—						
	Current Account at Bank	75	17	2			
	Deposit Account at Bank	30	10	6			
	Deposit Account Post Office Savings Bank	616	14	0			
903					723	1	8
£903					£923	1	8

Account

£		£	s.	d.
—	By Postage on Library Books	1	2	1
50	,, Balance at 30 April 1955	50	4	4
£50		£51	6	5

Special Accounts
(Trust and Reserve Funds)

RECEIPTS	£	s.	d.	£	s.	d.
To Balance at 1 May 1954 :—						
Westwood Fund	158	2	6			
Trail Award Fund	33	2	0			
Crisp Award Fund	55	16	1			
Hooker Lecture Fund	196	13	8			
Goodenough Fund	43	11	5			
Minchin Fellowship Fund	19	10	5			
Carnegie Corporation Grant	419	3	7			
Reserve for Publications Fund	2890	5	3			
Auckland Univ. Grant (Chapman)	500	0	0			
				4316	4	11
Transfer from General Account for Publications Fund				1100	0	0
Interest on Investments (gross) :—						
Westwood Fund	10	17	4			
Trail Award Fund	3	11	6			
Crisp Award Fund	13	19	0			
Hooker Lecture Fund	21	18	0			
Goodenough Fund	8	12	8			
Minchin Fellowship Fund	3	0	0			
Staff Pension Fund	9	15	8			
				71	14	2
				£5487	19	1

PAYMENTS	£	s.	d.	£	s.	d.
By Trail Award and Medal				31	19	3
,, Printing—Hooker Lecture Proceedings 164(1)				90	10	1
,, Illustrations—Journal Zoology (Westwood Fund)				88	16	0
,, Staff Pension Fund :—						
Purchase of £9 17*s.* 2*d.* 3 per cent Savings Bonds 1955–65				9	15	8
,, Balance at 30 April 1955 :—						
Westwood Fund	80	3	10			
Trail Award Fund	4	14	3			
Crisp Award Fund	69	15	1			
Hooker Lecture Fund	128	1	7			
Goodenough Fund	52	4	1			
Minchin Fellowship Fund	22	10	5			
Carnegie Corporation Grant	419	3	7			
Reserve for Publications Fund	3990	5	3			
Auckland Univ. Grant (Chapman)	500	0	0			
				*5266	18	1
				£5487	19	1

* Including £4181 5*s.* 10*d.* in Post Office Savings Bank.

Investments on 30 April 1955

General Account

£	s.	d.			*Market value 30 April 1955* £	s.	d.
1000	0	0	3½ per cent London County Consolidated Stock 1958–68	@ 94½	945	0	0
1548	8	9	British Transport 3 per cent Guaranteed Stock 1978–88	@ 80½	1246	10	0
720	0	1	3½ per cent War Loan, 1952 or after	@ 81½	586	16	1
1000	0	0	2½ per cent Defence Bonds	@100	1000	0	0
2199	18	6	4 per cent Australian Stock 1961–64	@ 99½	2188	18	6
200	0	0	3 per cent War Stock 1955–59	@ 97½	195	0	0
1139	13	0	3 per cent Savings Bonds 1955–65	@ 92½	1054	3	6
3260	1	3	2½ per cent Consolidated Stock	@ 60½	1972	6	9
176	19	3	3 per cent Savings Bonds 1960–70	@ 87½	154	16	10
274	5	5	3 per cent Treasury Stock	@ 71½	196	2	1
218	15	4	3½ per cent War Loan 1952 or after	@ 81½	178	5	10
					£9717	19	7

Library Account

£	s.	d.			£	s.	d.
471	18	9	British Transport 3 per cent Guaranteed Stock 1978–88 (Bentham Bequest)	@ 80½	379	18	2
103	12	5	Surrey County 3 per cent Stock 1961–66 (Wakehurst Bequest)	@ 91½	94	16	3
191	12	7	4 per cent Australian Stock 1961–64 (Walker & Morey Bequests)	@ 99½	190	13	5
107	2	1	2½ per cent Consolidated Stock (Stebbing Bequest)	@ 60½	64	16	0
530	0	0	3 per cent Savings Bonds 1960–70 (Tagart Bequest)	@ 87½	463	15	0
1414	7	11	2½ per cent Consolidated Stock (Flintoff Bequest)	@ 60½	855	14	2
					£2049	13	0

Special Accounts

	£	s.	d.			£	s.	d.
£1063 10 7	232	5	0	Metropolitan Water Board 3 per cent " B " Stock(Westwood Bequest)	@ 77½	179	19	11
	667	14	2	,, ,, (Hooker Lecture Fund).	@ 77½	517	9	6
	163	11	5	,, ,, (Goodenough Fund)	@ 77½	126	15	4
	557	12	1	2½ per cent Consolidated Stock (Crisp Award Fund)	@ 60½	337	7	0
£380 10 6	156	7	2	,, ,, (Westwood Fund)	@ 60½	94	12	0
	74	14	6	,, ,, (Hooker Lecture Fund)	@ 60½	45	4	0
	149	8	10	,, ,, (Goodenough Fund)	@ 60½	90	8	4
	323	14	10	3 per cent Savings Bonds 1955–65 (Staff Pension Fund)	@ 92½	299	9	2
	9	17	2	,, ,, ,, 1955–65 (Staff Pension Fund)	@ 92½	9	2	4
	100	0	0	,, ,, ,, 1960–70 (Minchin Fund)	@ 87½	87	10	0
	102	3	11	3½ per cent War Loan 1952 or after (Trail Award Fund)	@ 81½	83	5	11
				F. C. STERN, *Treasurer.*		£1871	3	6

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the year ended 30 April 1955 and found them correct. We have verified the Investments and Bank Balances.

18 May 1955.

W. B. KEEN & Co., *Chartered Accountants,*
Finsbury Circus House, Blomfield Street, London, E.C.2.

R. B. SEYMOUR SEWELL,
H. R. HEWER,
F. L. BALFOUR-BROWNE,
C. R. METCALFE,
ERROL I. WHITE,
Audit Committee.

Trust and Reserve Funds

I have already mentioned the Publications Reserve and the transfers from the Hooker Lecture and Westwood Funds. There is also the Trail Award and Medal presented last year; it is expected that the £500 received from Auckland University towards the cost of Professor Chapman's paper on New Zealand Algae, being published in the *Journal, Botany,* will be expended this coming year when it is hoped the paper will be issued.

Investments

£185 Compounders' Fees has been invested in £218 15*s.* 4*d.* 3½% War Loan and a further £44 Compounders' Fees has been invested since these Accounts were printed.

I should like to thank our General Secretary, Mr. O'Grady and our Clerk, Mrs. Ziegler, for the excellent manner in which the accounts have been kept, and for the conscientious way in which the work has been done.

If any Fellow wishes to ask any questions on these accounts, I will do my best to answer them.

Answering a question put by Dr. C. T. Prime on the possibility of the Society investing its Funds in other than Government Securities, the Treasurer replied that this was being considered by the Council in consultation with the professional Auditor.

On a motion by Dr. J. Ramsbottom, O.B.E., seconded by Lt.-Col. W. P. C. Tenison, D.S.O., the Report and Statement of Accounts were adopted.

In handing the Linnean Gold Medal to Mr. Ronald Graham Kerr, who was present on behalf of his father, the President spoke of Sir John Graham Kerr's contributions to Zoology and of the pleasure it afforded him personally that Sir John had been selected for the Award of the Medal.

THE PRESENTATION OF THE LINNEAN GOLD MEDAL

It does not very often happen that a Student is in the position of being able, in his capacity of President, to hand the Gold Medal of a Learned Society to a recipient who was in days gone by one of his teachers: and I had greatly looked forward to doing so this evening, for when I entered Christ's College, Cambridge, 56 years ago, Sir John Graham Kerr was then a Fellow of the College and was also a Demonstrator in the Department of Animal Morphology, as it was then termed. It was a very great disappointment to me when I heard about a fortnight ago that Sir John is now nearly totally blind and so is unable to be here in person. He has deputed his son, Mr. Ronald Graham Kerr, to receive the medal for him.

At the very commencement of his career Sir John carried on the Linnean and Darwinian tradition of Field Natural History by making an expedition in 1889 to 1891 to South America in order to study the Pilco Mayo River region, and following his return from there he joined Christ's College as a Scholar taking his Degree of B.A. with 1st Class Honours in 1896. During the next two years, in 1896–97, he carried out a second expedition, to the Gran Chaco, to study the little-known Lung-Fish, *Lepidosiren*; and on his return he was elected a Fellow of Christ's College and was appointed a Demonstrator in the Department of Animal Morphology, a post that he continued to hold for the next three years that coincided exactly with my own period of study as an undergraduate.

In 1902 Sir John was appointed Regius Professor of Zoology in the University of Glasgow, a post that he held for thirty-three years, and in the same year he was elected to be a Fellow of this Society. As Sir John himself has told us (*Vide* J. Graham Kerr, 1932, Archaic Fishes—*Lepidosiren, Protopterus, Polypterus*—and their bearing upon problems of vertebrate morphology. *Janaische Zeitschrift für Naturwissenschaft*, Vol. 67.) he determined as early as 1897 to make Vertebrate Morphology his main life's work and he set himself the task of doing what he could towards filling up the gaps in our knowledge of certain of the more archaic representatives of the phylum Vertebrata, particularly conspicuous in the case of the Dipnoan Fishes, and of their developmental stages. His investigations into the early embryology of *Lepidosiren* and *Protopterus* are classics, and the flow of research which has come from him and his pupils bears witness to his energy and enthusiasm for Zoology during the years in which he occupied the Regius Chair. The value and importance of his work was early recognized by his election in 1909 to the Royal Society.

At an age when most men are looking forward, albeit somewhat reluctantly, towards retirement, he was called to another sphere of activity, for in 1935 he was elected Member of Parliament for the Combined Scottish Universities. Here again he displayed that well directed energy, which has been so signal a feature of his life, and the present firmly established success of the Parliamentary Science Committee is due in no small measure to him. As early as 1914, at the commencement of the First World War, he advised the Admiralty of the advantages to be gained by ‘ dazzle ’ camouflage for ships at sea, and both before and during the Second World War he perseveringly advocated a rational and scientific approach to this practice, and the success achieved was due almost entirely to his advocacy over a period of years. During the period from 1941 to 1949 he was Chairman of the Advisory Committee on Fishery Research. During the course of his distinguished student career he gained a number of prizes; in 1896 or 7 (I have so far been unable to discover the actual year of this award) he was awarded the Darwin Research Prize by Christ's College ; in 1898 he was awarded the Walsingham Gold Medal by the University of Cambridge and in 1904 he was awarded the Neil Prize by the Royal Society of Edinburgh. In later years his pre-eminence was recognised by a number of learned Societies : in 1906–09 he was President of the Royal Physical Society of Edinburgh, and in 1937–38 he was a Vice-President of the Royal Society of London. In 1935 the Honorary Degree of L.L.D. was conferred upon him by the University of Edinburgh and in 1950 the University of St. Andrew's followed suit. In 1946 he was elected an Associate Member of the Royal Academy of Belgium and in 1939 he had the honour of Knighthood conferred upon him by his late Majesty King George VI.

In awarding Sir John Graham Kerr the Linnean Gold Medal we are not only honouring one who by his original research has shown himself to be a distinguished Scientist and a most able and stimulating teacher, who in later years has advanced the interests of our Science, but we are also honouring ourselves by including among the number of our Medalists the Doyen of British Zoologists.

In conclusion I thank you, Mr. Graham Kerr, for coming here this afternoon to receive the Medal on your father's behalf : and I ask you to convey to him our deep sympathy with him in his affliction and our warm affection for him, both as an eminent Scientist, a former Fellow of this Society and a personal friend of long standing.

Mr. Ronald Graham Kerr read a message of thanks from his father.

The General Secretary presented his Report.

GENERAL SECRETARY'S REPORT

List of the Society.

Since the last Anniversary Meeting the Society has lost 35 members. The detailed statement is as follows :—

13 *Fellows by Death :*

Sir John Stanhope ARKWRIGHT.
Henry ATKINSON.
Richard Eric Defoe BAKER.
William Charles BARTON.
Henry Augustus Hammond DUNN.
Arthur George GREGOR.
James JACK.
Thomas JOHNSON.
William Thomas MATHIAS.
Eleanor PEARSE.
Edward Stuart RUSSELL.
Rosamond Flora SHOVE.
Robert Vernan Giffard WOOLLEY.

4 *Foreign Members by Death :*

Liberty Hyde BAILEY.
Albert Francis BLAKESLEE.
Pierre TEILHARD DE CHARDIN.
August Adrian PULLE.
Herman Augustus SPOEHR.

1 *Associate* honoris causa *by Death :*

William Robert SHERRIN.

8 *Fellows by Withdrawal :*

John Macqueen COWAN.
Benjamin Thorton CROMWELL.
Christopher Leighton HARE.
James Hartley MURGATROYD.
Hugh Victor NEWBY.
Leo SACHS.
John Edward Miles WILLIAMS.
Hector Albert LONGMAN.

9 *Fellows by Removal for non-payment of Annual Contributions in accordance with Bye-Laws, Chap.* 2, *Sect.* 4 *:*

G. ABDIN.
Frank David ARMITAGE.
Sachindra Nath BENERJEE.
Prakash Chandra JOSHI.
James William MATTHEWS.
Mannath Devidas MENON.
Peter El LYE.
Gopal Singh PURI.
Helen M. TOWNLEY.

During the Session, 36 Fellows, 3 Foreign Members, 1 Associate *honoris causa* and 5 ordinary Associates have been elected. The number of Fellows on the List is 813 with a further 13 Fellows elected but not yet qualified. Foreign Members 49, Associates *honoris causa* 25 and ordinary Associates 27. 4 ordinary Associates have been elected Fellows during the year and 6 have withdrawn or their term of Associateship expired.

The Library.

Between 1 May 1954 and 30 April 1955, 26 Books have been purchased, 31 books and 141 parts of periodical publications and 73 reprints have been presented. During the same period the number of volumes bound was 544. The number of books borrowed was 1,083—by Fellows and Associates 843 and 240 by the National Central Library. 580 signatures were recorded in the Library Visitor's Book.

The Linnaean and Smithian Collections have been consulted by 46 Visitors during the Session and the Curators have removed specimens from the Linnaean

Collections to either the British Museum (Nat. Hist.) or Royal Botanic Gardens, Kew, on 20 occasions for critical examination.

The Society's collections of Correspondence and miscellaneous MSS. have been consulted frequently during the Session.

The PRESIDENT gave his Annual Review of the Society's activities.

THE PRESIDENT'S REVIEW

During the past Session, our 167th., the usual number of Meetings has been held. The work entailed in organising these meetings has, as usual, fallen on our two Secretaries, Dr. George Taylor and Mr. H. R. Hewer, to whom our grateful thanks are due. The average attendance has been, according to the number of signatures on the attendance forms, between 50 and 60.

During the Sessions we have been priviledged to hear from Mr. F. Evans, the Leader, an account of the ' Petula ' expedition across the Atlantic Ocean and he also very kindly gave us at the President's Reception the première showing of the film and a running commentary on their work. We have had two symposia on problems concerning fresh-water Biology, the first by Mr. K. A. Pyefinch and his colleagues of the Brown Trout Research Laboratory, Pitlochry, and the second by Dr. T. T. Macan and his colleagues from the Freshwater Biological Laboratory, Lake Windermere. We were also given by Professor Irene Manton and Dr. J. R. G. Bradfield a most interesting account of their work on Flagella Structure, illustrated by lantern slides of their observations with the Electron Microscope ; and this must have brought home to all of us who were present the immense complexity of even such a minute structure as a single flagellum. I may also mention the account given by Mr. J. W. S. Pringle, M.B.E., F.R.S., of his studies " On the Evolution of Cicada Song " that was accompanied by records of the actual song of several different species, Professor J. Heslop Harrison's talk on " Natural Hybridization and its consequences in British Dactylorchids ", and Dr. C. F. A. Pantin's paper on " Terrestrial Nemertines and Convergent Evolution ".

The President's Reception on 2 December was, as usual, a great success and our thanks are accorded to all who contributed to the exhibits and to the tasteful decoration of our Rooms.

During the year the Society has been invited to be represented at a number of Meetings of National, Foreign and International bodies. In June we received an invitation from the Sociedad Ameghinian de Ciencias Naturales e Instituto de La Historia Americana of Argentina to send a Representative to their Centenary Celebrations that were to be held in September and we sent them a letter of congratulations. The Society appointed Dr. George Taylor to represent us at the Meeting of the Société Botanique de France that was held at the Sorbonne, Paris, in July and he presented an Address from us to that Society. At the General Assembly of the International Union for the Protection of Nature that was held in Copenhagen in August/September we were represented by Mr. E. M. Nicholson, C.B., and in this connection I may mention that a short time previously a letter had been received from Miss M. A. Brooke, F.L.S. from Sarawak, in which she enquired whether we could make some official representation against the wanton destruction of birds and other animal life by the population: copies of this request were sent to Mr. Nicholson and to the International Union. At this Meeting Mr. Nicholson was asked to convey to this Society an invitation for us to be represented at their next Meeting, which is to be held in Edinburgh in 1956. We appointed Dr. George Taylor to be the Society's Representative on the British

Co-ordinating Committee for Nature Conservation, and we also appointed him to be the Society's Representative on the Royal Society's British National Committee for Biology; we are also represented on this Committee by Dr. C. F. A. Pantin, F.R.S. who is the Chairman. Finally Mr. J. S. L. Gilmour and Mr. E. Milne-Redhead were appointed to represent us at the Meeting of a Committee of the Botanical Society of the British Isles that was held to discuss the need for Autecological Studies of British Plants.

During the past Session we have continued to co-operate so far as we can with other Scientific Societies and Organizations and the use of our Rooms has been placed at the service of the following 14 Societies and Associations :—London Natural History Society, Malacological Society, Herpetological Society, South London Entomological Society, Botanical Society of the British Isles, Challenger Society, Ray Society, Biological Council, British Ecological Society, Association for the Study of Animal Behaviour, Amateur Entomologists' Society, Freshwater Biological Association, The British Association and the Systematics Association. In addition under the University Extension Lecture Scheme in conjunction with the London Natural History Society two courses of Lectures were given in our Meeting Room :—on " The Scientific Study of Birds " (10), and " The structure and uses of Wood " (12).

Ten years ago our then President, Mr. A. D. Cotton, O.B.E., in his Presidential Address pointed out that thirteen Societies or Associations had been permitted to use our rooms for their Meetings and he also drew attention to the fact that we had been approached by the Biological Council with the suggestion that the Linnean Society should take an active interest in the aims of the Council, one of their suggestions being that their members should have the use of the Society's rooms, the use of our Library for reference, and attendance at our Meetings and that we should also provide accommodation for their Secretariat; or to put it concisely that their Members should have most of the advantages enjoyed by our Fellows without actually joining us. During the past year we have been approached unofficially by another Society (The Biochemical Society) with a somewhat similar suggestion, and we have been asked to consider whether a close connection between themselves and us might be brought about. Among other things they enquired whether we could provide them with housing accommodation for their Library and Office. We are ourselves hard put to it to find the necessary accommodation for our ever expanding Library and the provision of space for another Society, no matter how much we may sympathize with their aims, is quite impossible. But in this connection there is another side to be considered and that is the conditions under which we are priviledged to occupy this part of Burlington House, for if we transgress these conditions we might, and probably would, be rendering ourselves liable to very considerable financial demands, such as the payment of Rates, from which we are at present exempt.

During the past year, 1954–55, we have issued 2 *Journals, Botany*; 1 *Journal Zoology*; 1 part, *Proceedings* and 1 *Synopsis of the British Fauna*.

Another part of our *Proceedings* awaits distribution by the Printers and in the Press we have 4 *Journals, Zoology*; 2 *Journals, Botany* and 2 parts of *Proceedings*.

I now propose to devote some time to, and deal at some length with, the work of our various Committees, as I think that it is very important that the general body of Fellows should have a clear idea of the difficulties under which we are to-day working.

I commence with the Library Committee.

THE LIBRARY COMMITTEE

This Committee has met regularly throughout the year and our thanks are due to the Members for the work that they have put in. During the year we have purchased a number of new books and periodicals, as well as receiving many publications in exchange or by presentation. New exchanges of publications have been arranged with the :—Instituto de Aclimatación, Almeria, Spain ; Polish Society of Botany, Warsaw, Poland ; University of Greifswald, Germany ; Red Sea Marine Biological Station, Cairo, Egypt and *Phyton*, an International Journal of experimental Botany, Buenos Aires, Argentina. The total number of serial publications that we obtain every year by purchase, exchange or as presentations is about 400.

Among the presentations made to the Society special mention must be made of the bequest in his will by the late Mr. A. A. Pearson F.L.S., of his Library, which comprised some 350 books dealing with Mycology, as well as numerous separates, letters, MSS. note-books : and the Royal Botanic Gardens, Kew, through the Zoological Society, has presented 29 unbound volumes of the *Memoirs of the Instituto Oswaldo Cruz* from 1929 to 1952.

The total additions to our library every year must thus be at least between 500–600 volumes : it is therefore not surprising that once again we are faced with the urgent necessity of providing more space to accommodate the increase. Ten years ago a Meeting was held at the Royal Society to consider the possibility of founding a central pool of certain periodicals such as the Proceedings of Academies or Societies, which include papers that deal with all the different branches of Science, and thus make a common library, the use of which would be available to all of us. This proposal was later overshadowed by the suggestion that a completely new habitat might be provided for certain Scientific Societies, of which the Linnean Society was one ; but more recently the Government have indicated that the economic conditions of the Country being what they are, it is unlikely that they would proceed with the schemes in the near future. Unfortunately, the mere existence of this scheme has tended to prevent other proposals being developed and so no action has been taken regarding any of the earlier suggestions. We are thus compelled to take such steps as we can to find accommodation for our ever expanding Library within the limits of our present quarters and this is a matter of very great difficulty for already our Library is hopelessly overcrowded and on some of the shelves books have had to be stacked in double or even treble rows ; and as, in consequence, the titles of the books in the second or third row on the shelves cannot be seen without the removal of volumes in the front row this adds enormously to the work of our Library Staff. Another difficulty that we have to face is the ever increasing cost of many publications that we have purchased in former years, and this rise is specially noticeable in the case of German publications. During the previous Session a Meeting of the Librarians of most of the Scientific Libraries in London was held in our rooms to consider whether it would be possible to relieve to some degree the financial strain by avoiding unnecessary duplication of these German periodicals. Another Meeting was held last June under the auspices of the Science Library and it was arranged that Librarians should be asked to submit lists of their holdings of such periodicals, after which a further meeting would be held, and there for the moment this matter rests.

A small Sub-Committee was set up, consisting of the Officers of the Society and, in addition, Mr. C. C. Hentschel and Mr. W. T. Stearn, to go into these matters and consider whether we could reduce the intake of certain periodicals which contain very little Biological material and which are readily available elsewhere in London, and perhaps sell some of our sets : Gage in his History of the Society* writes " Some of the publications of certain Academies and Societies contain both non-biological and biological papers, and sets of complete volumes of such publications occupy space out of proportion to the pages in them of direct interest to the Society. This was recognized more than sixty years ago, when the Librarian was authorized in 1872 to separate the Natural History papers in the publications of certain Academies and Societies for binding, but in fact that not entirely satisfactory experiment has never been practised ". It is thus clear that the problem of what to do with these very bulky and largely non-biological publications is no new one and once again this Sub-Committee puts forward the same suggestion, namely that in the case of such publications as the " Comptes Rendus " and the Transactions of National Academies we might break up the issues and keep only such parts as deal with Biological subjects, and after a period of years have these parts bound together, selling the rest of the paper for repulping. This would to some extent reduce the cost of binding and would very considerably reduce the amount of shelf space now required for housing these often very large volumes. But this procedure would entail a very great amount of work and as an alternative it was suggested that possibly the Royal Society might approach these other bodies and ask them whether they would consider publishing their periodicals in two series, biological and non-biological, as the Royal Society itself does: and there for the moment the matter rests.

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* A History of the Linnean Society of London, by A, T. Gage, 1938, p. 132.

Another suggestion put forward is that in the case of certain publications that are very bulky and which are easily available in a number of other Libraries in London, but which contain matter that is largely of only transient interest, such as ' Nature ' and ' Discovery ', we should keep only more recent volumes, covering the last five or ten years. Such a plan would also free very considerable space in the Library shelves.

Some 27 years ago our Society agreed to join the Outlier Library Scheme by which books from our Library could be borrowed through the National Central Library by other Libraries for individuals who were not Members or Fellows of Societies or Institutions from which the volumes could be obtained. We were then given a grant of £2,000 towards our own Library with the proviso that we were to spend not less than £500 per annum, on the maintenance of our own Library. At that time it seems to have been thought that the actual number of books borrowed from us would be relatively small: but a recent review of the numbers borrowed from the various libraries under the scheme has revealed that we are the third highest in the list, being surpassed only by Science Museum Library and the Library of the London School of Hygiene and Tropical Medicine, and the number is roughly equivalent to that of books borrowed by our own Fellows. All this has resulted in a considerable increase in the wear and tear of volumes and the consequent need for rebinding, so that our expenditure on this has in the last few years trebled. Your Council has informed the National Central Library that unless adequate financial support can be assured to us we must withdraw from the scheme.

A number of volumes that are part of the original Library of Linnaeus are now getting into such a condition that they are in urgent need of rebinding and arrangements are being made to have this done, and at the same time the Library Committee recommend that certain of these books should be withdrawn from consultation and that instead anyone who wants to consult them should either have a photo-copy made from the micro-film that we possess or should use the film with a viewer, thus avoiding, so far as is possible any further wear and tear on these precious volumes.

The Finance and General Purposes Committee

This Committee met in November last year. There is a constant rise in the cost of practically every branch of activity of the Society. I have already referred to the increase in the cost of rebinding and of purchasing certain of the publications that we have hitherto taken ; and, in addition, other Societies, being afflicted with the same financial difficulties, have informed us that they must in future withdraw from exchange and that if we desire to continue taking their publications we must pay for them. Other increased expenses are for heating and lighting, the salaries of our Staff and the cost of printing our Notices and Publications ; and as regards this latter item we have recently received from our Printers a notice that their charges are now to be raised by a further 10 per cent. The combined effect of all these has given rise to considerable anxiety. For some years we have been fortunate to obtain through the Royal Society a very substantial grant from the Government's Grant-in-Aid Fund towards the cost of our Publications ; in 1951–52 we received £750, in 1952–53 £1,250, last year we were granted £950 and this year we have been granted £1,000 and for this assistance we are deeply grateful ; but as our Treasurer has already informed you, it has now been hinted that we must not in future years look upon such aid as something that can be taken for granted and that it is time that we took steps to improve our financial position.

In the present circumstances it is quite impossible to resume our pre-war rate of publication and our expenditure on the Library ; and I may, perhaps, as one who spent many of the earlier years of my Fellowship abroad, remind you that for those Fellows who either live in remote parts of this Country or abroad and so cannot attend our Meetings, the receipt of our publications is one of the most important benefits that they can enjoy as a result of joining the Society.

The Finance and General Purposes Committee has now considered what steps can be taken to improve our Financial position and they urged that a special drive should be made in an endeavour to increase the number of Fellows who arrange for the payment of their Annual Contribution by entering into a seven-year contract, thereby enabling the Society to recover the Income-Tax on the amount ; in support of this proposal I sent to every Fellow of the Society resident in this Country a personal letter in which I urged them to do this. I am very grateful for the response that has been made and I am informed that 120 Fellows have agreed and 51 have already signed new Contracts : but even if two-thirds of all the Fellows residing in Great Britain and Northern Ireland did so, and it is only to such Fellows that the income tax concession can apply, there would still be a gap in our Budget.

Some years ago the Zoological Society withdrew the free issue of its publications to Fellows, and more recently the Royal Society has asked Fellows to relinquish their right to the free issue of one series of their publications, only retaining their right to the other, while at the same time it was arranged that they should be given free copies of any particular paper in the relinquished series if they applied for it. The Committee has placed before you alternative schemes, in one of which the same annual subscription as has existed since 1922, namely £4, is retained but the only free issue of the Society's publications would be the *Proceedings* ; while in the other the subscription would be raised to £5, and Fellows in this Country would receive the *Proceedings* and either the *Botanical* or the *Zoological* Journal, but not both. Under both schemes Fellows residing abroad would still be allowed to receive gratis both *Journals* if they so desired. Fellows were asked to fill up a form in which they expressed their preference for one or other of these suggestions and when a sufficient number of replies has been received the Council will put a definite proposal before the Society.

COMMITTEE OF INSPECTION OF THE LINNAEAN COLLECTIONS

In our Bye-Laws it is laid down that the Council for the time being shall appoint a Committee of Inspection on the condition of the Linnaean Collections and that it shall report to the Council prior to the Anniversary Meeting. Last year this was done and the Council also appointed two Curators. Mr. W. H. T. Tams, A.L.S. and Mr. N. Y. Sandwith, F.L.S., for the Zoological and Botanical Collections respectively, and in the Report that was submitted it was noted that the general condition of the greater part of these Collections was good, but that considerable rearrangement was desirable so as to facilitate the consultation of the collections by *bona fide* research-workers. This year a somewhat larger Committee was appointed, consisting of the Officers of the Society, the two Curators and in addition Dr. A. Tindell Hopwood and Mr. E. Milne-Redhead. We met on 16 December and carried out a thorough inspection. We reported that both the Botanical and the Insect Collections were in excellent order: the Mollusca collection is essentially in the state in which it was left by the eminent Conchologist, Sylvanus Hanley, in 1880, but that owing to the enforced move of the whole collection for safety during the war it had become badly disarranged: in his History of the Society, Gage noted that Hanley had unfortunately removed many of the specimens from the small metal cases in which Linnaeus had placed them and which originally bore the numbers corresponding to the MS. catalogue of the Museum Ulricae, and, what is still more unfortunate, Hanley also glued many of the specimens on to small wooden blocks, which thus entirely prevents any examination of the under surface. The Reptile Collection is also in a state of confusion and is inadequately accommodated. The Fish Collection, in the same order as A. C. L. Gunther, the then President, left it in 1898, is inadequately preserved in glass-topped boxes without proper protection. Finally, we are sorry to have to report that the Crustacea Collection is in a shocking state.

We also took the opportunity of examining the Smithian Collection: this was found to be in good order, with the exception of the Mosses, Lichens and unincorporated Fruits, which are at present inadequately housed in the old Tea-room.

I need hardly point out to Fellows of the Society that these Collections are some of the Society's most valuable possessions and it is our duty to ensure that they are adequately looked after and most carefully preserved, while at the same time providing facilities for *bona fide* research-workers and experts to examine the collections under adequate supervision. We have recommended that the Crustacea collection requires immediate attention by an expert in order to salvage as much as possible and to preserve the valuable specimens, which should be placed in glass-topped boxes. The Mollusca collection should be consolidated and arranged numerically according to the 10th. Edition of the *Systema Naturae*; and those specimens that have been mounted should be freed from their wooden tablets and, if possible, be replaced in their original containers, a number of which we still possess, or in glass-topped boxes. The type specimens of the Fish should each be placed in a separate container, provided with an insect repellant; and the Reptile collection should be rearranged and placed in separate boxes.

In addition to the work on the Linnaean Collections, the Mosses, Lichens and Fruits of the Smithian Herbarium should be arranged and boxes provided for their reception, while other miscellaneous collections should be adequately catalogued. To carry out all these recommendations of the Inspection Committee it will be necessary to obtain the collaboration of Specialists in the various groups and will I fear entail the expenditure of a considerable sum of money: but I would urge that the work be put in hand as soon as possible and that it should be completed within the next three years. I am glad to be able to announce that this work is already in hand and experts from the British Museum (Natural History) have examined the Reptile, Fish and Mollusc Collections.

While this Committee was carrying out its inspection of the Society's Collections we also took the opportunity to examine the state of the Stock-Room in which our publications are housed. Here too a great deal of work is required. The copies of past publications are in urgent need of re-sorting, stock-taking and re-arranging, to say nothing of dusting; and we have suggested that during the summer we should try to obtain the help of students from the various colleges in London, or perhaps elsewhere, who for a modest payment will come to our Rooms and carry out the necessary work.

The reason why I have urged that the work on the Linnaean Collections should be completed within the next three years is that in 1958 there will certainly be a very great influx of Visitors to our Rooms who will want to see these Collections.

I presume that every Fellow of this Society knows that the year 1958 is of very great interest and importance to us for it is the Bicentenary of the publication of the 10th Edition of Linnaeus' great work, the *Systema Naturae*, on which our present system of Nomenclature is based, and it is also the Centenary of the Meeting of this Society on 1 July 1858 at which were read the two papers by Charles Darwin and Alfred Russell Wallace respectively, in which they propounded their Theory of Evolution. These two anniversaries are of great interest to all Biologists throughout the world and it is because of this that the International Congress of Zoology has arranged to meet that year here in London, under the Presidency of Sir Gavin de Beer, F.R.S., F.L.S. Other Societies, such as the Royal Geographical Society, the Geological Society and the Royal Society, are proposing to have their own celebrations. An Advisory Committee for the International Congress has been set up, on which this Society is represented and the Council have appointed Dr. C. F. A. Pantin, F.R.S. In order to make plans for the proper celebrations by us of these two Centenaries and to co-ordinate these with the Celebrations of other Bodies, we have appointed a special Sub-Committee to explore the whole matter and make recommendations: the Members of this Sub-Committee are

The President and Officers of the Society.
Dr. C. F. A. Pantin, F.R.S.
Sir Gavin de Beer, F.R.S., President elect of the XVth International Congress of Zoology.
Dr. L. Harrison Matthews, F.R.S.
Dr. Edward Hindle, F.R.S.
Dr. H. W. Parker.
Dr. W. E. Swinton

with power to co-opt other Members, if desired. A number of ways by which these Centenaries can be suitably celebrated are now under consideration and in due course this Committee will place their suggestions before the Fellows.

Before I vacate this Chair for the last time as your President I must express to the Members of Council my very grateful thanks for the kindness and consideration that they have shown me during my period of Office and on behalf both of myself and all the Fellows of the Society our thanks for the way they have carried out their duties. I must also express my very deep gratitude to those Fellows who have held Office during my Presidency, to Col. F. C. Stern, our Treasurer, Dr. A. Tindell Hopwood and Mr. H. R. Hewer, our Zoological Secretaries and Dr. George Taylor, our Botanical Secretary. As you will have realized our Secretaries have been much occupied with duties in other spheres and the thanks of all of us are due to them for the devoted manner in which they have carried on the Society's business. Our Treasurer, Col. Stern, has also been much occupied with duties in another sphere; but he has continued to conduct the financial affairs of the Society in a manner that we are in danger of regarding as only to be expected, but that we must not take for granted, and a very hearty vote of thanks is due to him from the Society as well as from myself. Our very grateful thanks are also due to our two Curators, Mr. W. H. T. Tams and Mr. N. Y. Sandwith, for the work they have put in, in looking after our Collections. I must also record the grateful thanks both of the Fellows in general and myself in particular to our Staff ; to Mr. T. O'Grady, our General Secretary ; to Mr. W. S. Warton, our Librarian, who was away owing to illness for some time during the early part of this Session but whom we are glad to have back with us again ; to Mrs. E. Ziegler, our Clerk and to Mr. B. Wislawski, our Housekeeper and general handy-man, for the way in which they have carried out their duties.

Lt.-Col. R. B. Seymour Sewell then introduced the President-Elect, Dr. H. Hamshaw Thomas, M.B.E., F.R.S., and handed him the Key to the Society's Iron Chest.

Dr. J. Ramsbottom expressed the thanks of the Fellows to Lt.-Col. R. B. Seymour Sewell for his valuable services to the Society during his term of Office as President and welcomed and congratulated Dr. H. Hamshaw Thomas the newly elected President.

The PRESIDENT-ELECT announced that he would appoint the following as Vice-Presidents for 1955–56 :—Mr. E. J. H. CORNER, F.R.S., Dr. A. TINDELL HOPWOOD, Lt.-Col. R. B. SEYMOUR SEWELL, C.I.E., F.R.S., and Colonel F. C. STERN, O.B.E., M.C.

The following papers were read in title :—

'The evolution of Arthropodan mechanisms, Part V.' By S. M. MANTON, F.R.S., F.L.S.

'The Dick Herbarium' By Sir GAVIN DE BEER, F.R.S., F.L.S.

Thereafter the Session 1954–55 was declared closed.

ADDITIONS AND DONATIONS
TO THE
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1954–55

Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

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BENEFACTIONS

LIST *in accordance with Bye-Laws, Chap.* 17, *Sect.* 1, *of all Donations of the amount or value of Twenty Pounds and upwards, received during the past five years.*

1951

The Royal Society : Grant-in-aid of publications, £750.
Mr. James Insch, F.L.S. : Bequest of Library of works on Tea.
Mr. John H. Robins : The collected correspondence of Richard Pulteney, F.R.S., F.L.S.

1952

The Royal Society : Grant-in-aid of publications, £1250.

1953

Auckland University College : Grant towards cost of Prof. V. J. Chapman's paper on New Zealand Algae in *Journal, Botany* (press), £500.
The Royal Society : Grant-in-aid of publications, £950.
Mr. J. D. Snowden, F.L.S.: Gift towards cost of paper on *Sorghum* in *Journal, Botany*, No. 358, £25.
Gift to Library Fund in Memory of Miss Maud Williams, F.L.S., £100.
Dr. Hugh Scott, F.R.S. : Cost of blocks for plates and £293 0*s*. 11*d*. towards cost of printing his Gughé Highlands paper in *Proceedings, 163*.

1954

The Royal Society : Grant-in-aid of publications, £1,000.
Mr. H. Womersley, A.L.S. : Gift towards cost of illustrations of paper in *Journal, Zoology*, No. 288, £20.
Mr. A. A. Pearson, F.L.S. : Bequest of Library of Mycological Works.
Imperial Chemical Industries Limited : Gift to the Library Fund, £21.

1955

The Royal Society : Grant-in-aid of publications, £1,250.
The Trustees of The Percy Sladen Memorial Fund : Cost of printing *Transactions*, Ser. 3, Vol. 1, Part 3, £625 3*s*. 6*d*.

OBITUARIES.

Valentin Alexandrovitch Dogiel, who had been Professor of Invertebrate Zoology in the University of Leningrad for 42 years when he died on 1 June 1955 in his 74th year, had a world-wide reputation as a protozoologist and parasitologist.

His most important work in protozoology was devoted to the parasitic ciliates (Ophryoscolecidae) of ruminants, the systematics, evolution and physiology of which were thoroughly revised by him. In general parasitology Dogiel was a pioneer of a new ecological approach to the host-parasite relations, especially the effect upon the parasitic fauna of changes in the environment and physiology of their hosts. The results of investigations in this field found practical application in the fisheries of the Soviet Union. Dogiel's vast erudition can be best appreciated in two publications, " General Protistology " (1951) and " Textbook of General Parasitology " (1941, 1947), which are outstanding original contributions to our knowledge of these subjects.

Though primarily a parasitologist, Dogiel also made noteworthy contributions to general zoology, and especially comparative anatomy. These studies were brought together in a monograph—which proved to be his " Swan song "—on " Oligomerization of Homologous Organs " (1954), in which he develops a new theory of evolution of the Metazoa. In addition to these books, Dogiel was the author of standard textbooks of " Comparative Anatomy of the Invertebrates " and " Invertebrate Zoology ".

And last, but not least, Dogiel was a first-class teacher, who created a school of biology from which numerous Russian, as well as some foreign workers (including the present writer), emerged.

Dogiel's scientific achievements were recognized by his election as Corresponding Member of the Academy of Sciences of U.S.S.R. in 1939 and Foreign Member of The Linnean Society of London in 1944, as well as by other honours and awards conferred upon him in his own country.

CECIL A. HOARE.

Col. **Charles Grey,** D.S.O. Born in 1875 he was christened Charles Hervey Hoare. A son of the old banking family of that name and a descendant of the creator of the famous 18th century Garden at Stourhead now owned by the National Trust. (Later in life to comply with testamentary obligations he assumed the surname of Grey instead of Hoare.) He was educated at Eton where he nearly reached the top of the School. On the outbreak of the Boer War he joined up and narrowly escaped death. In the First World War he commanded a battalion with distinction, was severely wounded and was awarded the D.S.O. Although 65 he made every effort to be reemployed in the army in the Second World War. He was not successful in view of his age and wound but managed to be appointed Commandant of an R.A.F. aerodrome. There have been few who have been so little conscious of fear . . . he told a friend that rifle fire never troubled him, but he did not like shelling. He had many friends, but was not of those who suffer an insult gladly and turn the other cheek. What he possessed above all was industry and enthusiasm, having put his hand to the plough nothing would make him turn back. His book on bulbous plants has been generously commended. At Hocke Edge in Kent he owned a nursery garden where he grew successfully many of the less common plants. The pleasure he got out of it outweighed the lack of profit and he was fortunately in a position to disregard the losses. In 1945 he moved to Malton, and it was there that he conceived the idea of a Northern Horticultural Society and of a garden more or less on the lines of Wisley but on a smaller scale, where those living between the Tees and Trent could see things growing under the generally colder conditions to which they were accustomed. Having formulated the idea he threw himself into the project with almost unbelievable enthusiasm. With his friends he was almost merciless. A donation received his thanks, but in the acknowledgement there was always a suggestion that so and so might have spared more. As to his own purse he drained it to the bottom and freely denuded his own garden of all of its best plants. Even if he had a bet on a race as he did sometimes, the loss would be his but the winnings went to the Society. That he was working against time was obvious to all and certainly to himself, there was no question of sparing himself for others. Even during the last two years when he was in constant pain and could not stand without support he went on writing, working to his very last. He was born a fighter and fought to the last ditch. Those who knew him hope that the garden he created at Harlow Car near Harrogate will be a lasting memorial to him and an ever increasing source of instruction and pleasure to those who live in the north country.

R. J.

Francis John Lewis, who died on May 24th 1955, had been a Fellow of the Society since 1900. He was born in London in 1875, and received his early training at the Royal College of Science and at the University of Liverpool. He was appointed Demonstrator in Botany at Liverpool in 1900, was Assistant Lecturer 1901–1907, and then Lecturer in Geographical Botany.

He was one of the first British Botanists to undertake research in plant ecology ; his first paper, published in the Geographical Journal in 1904, gave the results of his survey of the vegetation of the basins of the rivers Eden, Tees, Tyne and Wear, with a vegetation map of the area. This work led him to investigate the plant remains in peat-mosses, and during the next eight years he devoted his spare time to an investigation of the sequence of plants in the peat of different parts of Scotland and of some areas in England and Iceland. He studied this sequence in about forty different districts, and obtained evidence of the changes in their vegetation, from which he concluded that several changes had occurred in the climate since the last ice-age. Moreover he found it possible to correlate the changes in the plant remains in most of the areas, showing that it was improbable that the sequences found were due merely to edaphic conditions, as many had thought. This work, which was based on the observation of tree stumps and macroscopic remains of plants, preceded the discovery that peat also contained well preserved pollen grains. His results were mainly published in the Transactions of the Royal Society of Edinburgh, and that Society awarded him its Neill Gold Medal in 1910. Although he may have been influenced overmuch by the views of Prof. James Giekie, his researches played an important part in the development of the study of post-glacial vegetation which has now proved so valuable and so far reaching. His papers attracted attention in Scandanavia, where the study of climatic changes since the last glacial period was being actively pursued.

Lewis collaborated with C. E. Moss in writing an article on " The Upland Moors of the Pennine Chain " for Tansley's *Types of British Vegetation* (1911). But his interests were not confined to studies of past and present vegetation ; he produced a paper on " Induced Variations in the Osmotic Pressure in the Leaves of Non-Halophytes " in 1912, as well as a note on the internodes of Calamites in the Linnean Journal for the same year.

A new epoch in his career opened in 1912, when he accepted appointment as the first professor of Botany in the University of Alberta, Edmonton, a post which he held until 1935. The creation of a new department, with staff, equipment and courses of study suitable for the students of this young university, was a very considerable task, especially during the period of the First World

War. When he was free to work in the field he commenced a pioneer survey of the vegetation of the Canadian Rocky Mountains, and of its distribution, contributing papers on the subject at meetings of the British Association in 1920 and 1924. With his students he carried out a general survey of the vegetation of the province of Alberta, which includes an immense area of forest, park-land and prairie ; they made more detailed investigations of the ecological features of certain regions in the province. This work was described in the Journal of Ecology in 1925 and 1926. He took up the study of the fungi which occurred on *Picea canadensis* and on other conifers. His interest in plant physiology found expression in a research with G. M. Tuttle on the osmotic properties of some plant cells at low temperatures (New Phytol. 1923) and on seasonal changes in the leaf cells of *P. canadensis*. With Miss Dowding he studied the anatomy of the buds of Coniferae.

On his retirement from Edmonton he was appointed Professor of Botany at the Fouad I University in Cairo, in succession to F. W. Oliver. Here again he was much concerned with the transfer of the small department to spacious new laboratories at Giza, and with the organisation of teaching and research. Once more he had to contend with the many difficulties created by a war on the frontiers of Egypt, but he maintained his vitality and his enthusiastic interest in the study of plants. During this period his researches were mainly directed to the study of the physiology of desert species, and especially to their ability to obtain their water from dew. This led to the question of the wettability of cell-walls in the mesophyll of leaves, a new problem, on which he published two short communications in *Nature*.

Leaving Egypt at the age of 71 he returned to England still fit and active. In 1947 he became visiting lecturer in plant physiology for a year at the Royal Holloway College, and he became connected with the publishing trade by acting as an advisory editor for the new editions of Chambers' Encyclopedia. Up to the time of his death he acted as a liason officer between the publishing firm of Macmillan and Company and the British Universities, paying frequent visits to botanical departments throughout the country.

He was first married in 1901, his wife died in 1927, and later he married Mitta Dickson, who survives him.

Francis Lewis had a very alert and original mind, a great interest in all aspects of plant science, and a charming and friendly personality. Although he spent much of his life abroad, he always maintained a keen interest in the Linnean Society, and he was also a Fellow of the Royal Society of Edinburgh. His lot was never an easy one, he had to contend with much greater difficulties than most men in a like position have to meet. But he never complained, and his enthusiasm remained undaunted. After leaving Liverpool his output of original research greatly diminished, but the work of the two departments which he helped to build up should form a lasting memorial to his enthusiasm, his energy and his tact.

H. Hamshaw Thomas.

Major **Albert Pam,** O.B.E. who died 2 September was a man who contributed much to the varied spheres which he made his own. This is not the place to speak of his distinguished career in the City of London but rather of his achievements in the world of Natural History.

In his " Adventures and Recollections ", published in 1945, he tells us that he was born on 28 June 1875 at Clapham Park, then a comparatively rural area where, at an early age, he started to collect animals, among them lizards and snakes. He gradually became an all-round naturalist and found that this hobby added great interest to his foreign travel. He spent much time in South America, particularly Venezuela and on one occasion imported in addition to reptiles, 13 species of mammals and 124 species of birds for the Zoological Society of London from Caracas. The Society, of which he was Treasurer from 1932 to 1945, conferred its Silver Medal on him in 1914.

At the same time he became a keen horticulturist, specializing in the Amaryllidaceae. He was one of the few to have had a plant genus named after him when in 1926 a superb new amaryllid was christened Pamianthe peruviana (Bot. Mag. vol. **156** tab. 9315) in his honour.

A member of the Council of the Royal Horticultural Society, he was awarded the Victoria Medal of Honour in 1943 and in 1944 he received from Oxford University the degree of M.A., *honoris causa.*

Those who enjoyed the hospitality of Wormley Bury, his beautiful home in Hertfordshire, will recall the fine collections of ducks on the lake and amaryllids in the greenhouses, though the author of these words particularly remembers a frame which housed the fruits of an unforgettable Greek tour in 1938 when he accompanied Major Pam, his wife and great ally Mr. E. A. Bowles in the Peloponnese and elsewhere. Friends in many different circles will miss a man whose rather grave exterior sheltered a lively sense of humour and a kind heart.

MARK OGILVIE GRANT.

Arthur William Rymer Roberts was born in Manchester on 1 December 1879. After some years at Windermere he was educated at Harrow Public School and Cambridge University, where he studied law. A short activity as a barrister only reinforced Rymer Roberts's predilection for scientific subjects and caused him to return to Cambridge and read biology as a postgraduate student. Applied entomology and agriculture fascinated him especially, and he kept up his interest in them until his death. He bought a farm at Crook near Kendal, after having successfully sat for the M.A. degree, but took up research work at Rothamsted Experimental Station during the 1914–1918 war. In 1920 he moved to Cambridge and, after a short period at the Zoological Laboratory, spent the rest of his professional life as a voluntary research worker at the Molteno Institute. After twenty years he withdrew from active entomological work and acquired " Applegarth ", a house with a large ornamental garden and apple orchard at Cartmel near Grange-over-Sands, where he keenly applied his agricultural and entomological knowledge to his trees and land. Recently he found the large garden and house somewhat burdensome and prepared for creating himself a less exacting home on a smaller beautiful site at Grange-over-Sands. In the middle of these preparations he died at Cartmel on April 9th 1955, 75 years old.

After having studied entomology under Prof. F. Balfour-Browne, Rymer Roberts took up the study of Aphids, reading in 1915 a paper " On two cases of parallelism in the Aphidae " before the Manchester Literary and Philosophical Society, preparing a leaflet on the life history, collection and preservation of this group for the Lancashire and Cheshire Fauna Committee, and later (1928) contributing a chapter on the life-cycle of the *Periphyllus* species to Theobald's work. At Rothamsted in 1916 he began research work on the life history of important wireworms, which work soon led him to study the morphological differences of the species involved. His four papers on *Agriotes* and *Athous* appeared from 1919–1928 in Annals of applied Biology (vols. **6**, **8**, **9** and **15**), and a fifth paper, dealing with the toxicity of organic compounds to wireworms, was published jointly with F. Tattersfield in Journal of agricultural Science 1920. At Cambridge Rymer Roberts prepared three papers on weevil larvae, published in 1926 (descriptions of some larvae of Adelognatha, in Ann. appl. Biol. **13**), 1931 (on the hatching from the egg, in Ann. Mag. n.H. (10) **8**), and 1936 (on the spiracles of first-stage larvae, in Livre jubil. E. L. Bouvier), and " A key to the principal families of Coleoptera in the larval stage" (1930, Bull. ent. Res. **21**).

The latter is undoubtedly his most important paper, as it represents the first key containing the bulk of the beetle families in the larval stage and employing modern comparative morphological characters. The order is divided into easily recognised artificial groups and, although the paper was somewhat eclipsed by Böving and Craighead's much more detailed " natural " key, which began to appear only twenty months later, his key is still much used, and some recent " easy " keys have drawn upon it freely. Rymer Roberts's second decade at Cambridge was devoted to a revision of the key to the families (never drafted) and to the preparation of an important paper on Erotylid larvae. The first part of the latter, containing a key to the subfamilies and species descriptions to two subfamilies, was published in 1939 (Trans. R. ent. Soc. **88**), and the descriptions and many drawings for the second part have been found among his notes given by his widow to the writer. A small paper on the larva of *Cryptohypnus* has been published in Proc. R. ent. Soc. (A) **31**, 1956. All these papers are models of thoroughness in text and illustrations and important contributions towards the morphology and classification of the groups concerned.

A. W. Rymer Roberts's personal characteristics were kindness, modesty and cheerfulness, and those who have had the privilege of meeting him or corresponding with him will not easily forget the pleasurable sentiment which every contact with him evoked. He took a prominent part in the unobtrusive religious and humanitarian work of the Society of Friends, ably and enthusiastically assisted by his wife, Mrs. Ruth Rymer Roberts née Gimingham, whom he married in 1920, and who survived him only nine months.

F. I. VAN EMDEN.

William Robert Sherrin died at East Dulwich on 22 March 1955 after a long period of declining health. He was born on 20 May 1871. On 6 March 1919 he was elected an Associate *Honoris causa* of the Linnean Society and until recent years attended meetings regularly, though modesty prevented him from taking a frequent part in discussions following papers.

His father was the artist John Sherrin and during the early part of his life Sherrin had many homes. As a youth he was regarded as weakly and on medical advice was ordered to spend as much time as possible in the open air. At that time his family lived in Thanet, and the days spent wandering round the coast and marshes near his home fostered an interest in natural history which was destined to dominate his thoughts and actions for the rest of a very active life. As an outlet for his interests and natural skill he set up in business as a taxidermist in Ramsgate until, in 1895, he was engaged as an articulator in the Department of Zoology of the British Museum (Natural History). He served the Trustees of the Museum for 52 years—first, as full time articulator in the Department of Zoology until 1919, then as part-time articulator until 1928 when he transferred to the Department of Botany as part-time assistant. He retired from the staff of the Museum on 17 October 1947. In 1919 he was appointed Curator of the South London Botanical Institute, of which he continued Curator and Secretary until his death.

Sherrin was a general naturalist in the fullest sense of the term. To his friends he constantly stressed the importance of having a " second interest " to avoid the risk of becoming stale but there was never a possibility that he would need the advice he offered. In fact, he had a dozen interests—mammals, birds, mollusca, lepidoptera, coleoptera, bryophytes and phanerogams were amongst the groups he studied, but there was hardly a branch of natural history from myxomycetes to astronomy which failed to attract his attention at some time. The ease with which he could switch his whole-hearted interest from one subject to another enabled him to work successfully for many years in the Department of Zoology in the morning and as a botanist in the afternoon and evening ; on the other hand, it made it difficult for him to concentrate on research in a limited field. He attempted this only for bryophytes.

His interest in mosses commenced at an early date and continued to the end and he said that it was first aroused by the beautiful tropical bryophytes used as packing for mammals sent to the Museum. The earliest specimens of mosses collected by Sherrin which have been traced were gathered in 1900 ; five years later he joined the junior section of the Moss Exchange Club, and the main club in 1906. In 1916 the School Nature Study Union issued his booklet on the *Study of Mosses in the London District*, which was illustrated by his own sketches. *An Illustrated Handbook of the British Sphagna* appeared in 1927, and from that time onwards he was a recognised authority on bog-mosses. He determined the *Sphagna* in Bauer's *Musci Europaei et Americani Exsiccati*, and acted as referee for *Sphagna* and other mosses for the British Bryological Society. From 1928 until he retired in 1947, Sherrin worked on the collection of bryophytes in the Department of Botany at the Natural History Museum and with his usual unbounded energy incorporated vast accumulations of mosses from many parts of the world. During this period he published a number of short papers on new or interesting bryophytes which came to his notice. These included a *Revision of the Genus Spiridens* and descriptions of mosses from Albania and Rhodesia. From 1925 he acted as librarian and curator of the British Bryological Society, of which he had the signal honour to be elected President in 1945 to cover the period of their Jubilee Meeting the following year.

Although Sherrin is most widely known and respected for his work on bryology, his influence in directions which received less publicity was perhaps of greater importance. His infectious enthusiasm was irresistable, and the more so because he could interest people in so many diverse groups. To young people he had a special charm and as Curator of the South London Botanical Institute he had outstanding success in interesting them and encouraging serious work. I have written elsewhere an appreciation of his achievements in this way. (*Proc.B.S.B.I.*, **1**, 553–6, 1955). During the early years of his curatorship he worked on the collections before breakfast, and again from 2 until 9 p.m. if there were no visitors. Even so, it took years to incorporate the accumulations and to get the herbaria into a state in which they could be easily consulted. At first he had the assistance of a mounter, but after a time he preferred to undertake the tedious work of mounting specimens himself. The British and European collections of flowering plants and ferns, then the algae, bryophytes, lichens, mycetozoa and conifers were mounted and arranged. Special collections of microscope slides, seeds, and lantern slides were got together. The library was arranged and catalogued, and an index to the *Journal of Botany* from the first number was prepared. His enthusiasm for adding to the facilities of the Institute remained to the end, but perhaps the last new collection to be started was that of specimens of planted trees and shrubs on which he worked with the aid of the late A. Bruce Jackson during the early years of the last war. Sherrin transformed the collections of the South London Botanical Institute to such an extent that few people using them today can realise how much they owe to his efforts.

Many fine mammal skeletons at the Natural History Museum remain as a record of the 33 years he spent on this work, and two mammals were named for him—*Nyctophilus sherrini* Thomas in 1915, and *Tatera sherrini* Wroughton in 1917 (the last is now sunk in synonomy). Shortly before his death he was made an Honorary Life Fellow of the Zoological Society of London, of which he had been a Fellow for many years. In 1942 he was elected a Corresponding Member (now Honorary Member) of the Botanical Society of the British Isles.

Sherrin was twice married—his first wife died in 1938—and he is survived by a son and daughter and his second wife. Deeply and sincerely religious, modest and retiring, his influence on many who knew him well was great. By the encouragement and help he gave so freely to others he made his greatest contribution to science. J. E. LOUSLEY.

Pierre Teilhard de Chardin, S. J., a Foreign Member of the Linnean Society of London since 1950, was born in the Auvergne on May Day, 1881, and died in New York on Easter Day, 1955. He was the fourth child of Emmanuel Teilhard and was of the sixth generation in direct descent from Marguérite-Cathérine Arouet, the sister of Voltaire. His childhood was passed in the neighbourhood of Clermont Ferrand where the numerous extinct volcanoes aroused in him a love for geology that remained with him all his life. In 1899 he entered the Society of Jesus as a novice and there the severe intellectual discipline characteristic of his Order went hand in hand with instruction in all branches of science, particularly geology and zoology. At the turn of the century he undertook field-work in Jersey (1901-1905), Egypt (1905–1908), and the Weald (1908–1912). This period, which included work at Piltdown with Sir Arthur Smith Woodward, was essentially formative : apart from writing short notes published by La Société Jersiaise and in the *Bulletin de la Société Scientifique du Caïre*, he spent his time gaining experience and collecting specimens for others to describe.

In 1912 Teilhard began to work regularly at the Muséum National d' Histoire Naturelle in Paris on the Lower and Middle Tertiary mammals of Europe. During the years 1912 to 1923, apart from the war, he described old but unpublished material from the Phosphorites of Quercy, the Sparnacian of Epernay, the Paleocene of Rheims, and, lastly, the mammalian microfauna discovered by Dollo in the Sparnacian deposits of Orsmael, Belgium. This work brought him into almost daily contact with Marcellin Boule, then Director of the Laboratory of Paleontology, and, a little later, with Abbé Breuil, both of whom carefully fostered his growing interest in fossil man and so helped to prepare him for his future work in Asia.

In 1923, Father Teilhard was posted to China to join the late Father Emile Licent, S. J., in his work of exploration and research. Apart from an expedition to French Somaliland and the Harrar in 1928-1929, he spent the next twenty-two years in investigations in the Far East. During that time he took part in the Central Asian expedition of the American Museum of Natural History (1930), the Haardt-Citroën expedition (1931–1932), the Yale–Cambridge expedition in central and northern India (1935–1936), and the Harvard–Carnegie expedition to Burma (1937–1938). In the course of his travels in China, he not only made complete geological sections from Harbin in Manchuria to the Indo-Chinese border, and from Shantung to the confines of the Pamirs, but he also studied the Quaternary volcanoes of Dalai Nor, the Eocene deposits of Ordos, the sunken basins of Tsingling, and other areas completely unknown to science until he and his colleagues visited them.

Teilhard's first love in mammalian palaeontology was for the Lower Tertiary faunas, but when he went to China his interests changed. Apart from a memoir on the Oligocene mammals of Ordos, practically all his work was directed towards unravelling the post-Pontian history of the mammals of North China. He studied the faunas of the Middle Pliocene of Yushé in Shansi, of the Villafranchian beds of Nihowan in Hopei, of the fissure fillings of Choukoutien, and of the Upper Pleistocene of Sjara-Osso-Gol. His were no mere descriptive memoirs ; because he had seen the deposits in the field, and investigated the cycles of sedimentation, he was able to take into account the physiography and climate at a given period and to describe the ecology of the fauna under review.

In addition to all this, Teilhard took an active part in planning and directing the excavation and research at Choukoutien, famous as the place of discovery of *Sinanthropus*. His particular responsibility was the stratigraphical, palaeontological and archaeological history of the deposit. This was no easy task, for the limestone massif contained six different series of fissures ranging in date from the Miocene to the Upper Pleistocene, each series with its own filling. Fortunately, fossil mammals were so abundant that he was able to date the different fissure systems and to correlate them with the river terraces and basins he had studied in other areas ; a remarkable result all too seldom achieved, even in Europe.

So far I have summarized some detailed notes that Fr. Teilhard compiled about six or seven years ago, but for his work and views on the genesis of rational humanity, on philosophy, and on theology, there is no such guidance. We who had the privilege of discussing these things with him, and of listening to his teaching, must rely on our memories and impressions, as well as on certain writings that circulated in typescript among his friends. Each of those writings was carefully finished and lovingly polished, for Teilhard was sternly self-critical, but they were intended to stimulate thought and discussion among those who were interested in the problems arising from the interplay of the earth-sciences, philosophy and theology, and were for private reading and study. When, some years ago, I ventured to say that it was a pity they should not be printed, he replied with that gentle firmness we knew so well that his paper " La structure phylétique du groupe humaine " (*Ann. Paléont.*, Paris, **37**, pp. 49–78) was all that would be published.

Theologian and savant, mystic and poet, he towered above his fellows as a giant. Not unnaturally he was often misunderstood, for few, if any, of his contemporaries had his massive mentality and clearness of vision. His philosophical and theological views were often criticized and quite unfounded charges of pantheism brought against him. Indeed, there was an unsuccessful attempt to delate him to Rome that his teachings might be condemned.

In so far as they took exception to his views on evolution, his would-be delators appear to have overlooked the dictum of St. Thomas, " The same sort of certitude is not to be expected in all fields of scientific enquiry. The well disciplined mind will not demand greater certitude than the subject will offer, nor be content with less ". The earth-sciences are inductive ; they argue *a posteriori*, from effect to cause, from the particular to the general. Consequently, and quite apart from the nature of the evidence, their degree of certitude is less than the certitude of mathematics where the arguments are *a priori*, a point often forgotten by scientists and theologians alike.

Teilhard was a man of great charm, one of the kindest and most humble of men. Himself the soul of honour, incapable of an unworthy thought or deed, he gave freely of the fruit of his experience in many fields of knowledge and asked for nothing but complete intellectual honesty in return. He never could understand the influence he had on others, an influence that he often found embarrassing, but when the history of his time comes to be written it may well be found that he did more to influence the development of French thought, and hence of European thought, than any other man of his generation. As one looks back over the whole life and work of this loyal son of his Church, and tries to realize how much richer the world is for his endeavours, there comes to mind the petition that runs like a refrain through the Vespers for the Dead, " Eternal rest grant to him, O Lord. And let light perpetual shine upon him ".

A. T. H.

Professor August Adriaan Pulle was born on 10 January, 1878, at Arnhem, where he attended the High Schol, and became interested in Chemistry and Botany. In 1897 he entered the University of Utrecht as a pharmaceutical student, obtaining his B.Sc. in 1899. His interest in Botany was re-kindled by the late Prof. F. A. F. C. Went, to whom he soon became Assistant. In 1902 he took his M.Sc., and went to Surinam as botanist in the Saramacca Expedition, returning in 1903 with a large collection of herbarium specimens. My first acquaintance with him was when, as a very serious young man, he came to Kew in the course of working out his collections, and entrusted the elaboration of the family Bignoniaceae to me. In 1906 he published his results in " *An Enumeration of the Vascular Plants known from Suriname* " which he presented as a thesis for his doctorate. This book formed the basis for the further study of the flora of Surinam.

He was soon appointed lecturer in systematic botany and plant geography at Utrecht, and obtained the stipend of the ' Buitenzorg Fund ' for a visit to Java. He also took part in the third Dutch expedition to New Guinea, 1912–13, which brought back extensive botanical collections. His appointment as Professor of Systematic Botany and Plant Geography at Utrecht in 1914 was a very happy one, enabling him to raise the Botanical Museum and Herbarium to the position it now occupies as one of the foremost Botanical Institutions in the World.

Pulle and his pupils wrote an extensive series of papers on the floras of Surinam and Malesia, on pollen analysis of peat deposits in the Netherlands, and on the vegetation of that country. He edited the " *Flora of Suriname* ". At the International Botanical Congress, Amsterdam, 1935, his genial and business-like work as Recorder enabled the Subsection for Nomenclature to get through its programme in the time allotted. He was elected Foreign Member of the Linnean Society in 1940. On the occasion of the International Botanical Congress in 1950, Pulle was in great form, even venturing to make a speech in Swedish at the final Plenary Meeting.

Pulle's wide interests included the phylogenetic inter-relationships of the families of Seed Plants : he regarded the other dicotyledonous orders as derived from the Ranunculales (*sensu lato*), and embodied his views in his " *Compendium van de Terminologie, Nomenclature en Systematiek der Zaadplanten* ", of which the third edition appeared in 1952 : he considered the apetalous and gamopetalous orders as descended from various polypetalous groups.

Pulle's health was undermined during the German occupation of Holland, when he suffered great privations. He died on 28 February 1955, after a long and painful illness. He was an excellent companion and a great gentleman.

Many of the data concerning Pulle's career have been summarized from the obituary notice by Prof. J. Lanjouw in *Taxon*, **4,** No. 3, pp. 54–57 (1955).

T. A. SPRAGUE.

THE STRUCTURE AND EVOLUTION OF THE ORGANS OF SOUND-PRODUCTION IN CICADAS

By J. W. S. Pringle.

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(With 11 text-figures.)

Introduction.

In the course of a recent investigation of the physiological mechanism of sound-production in the male cicada (Pringle, 1954) it became necessary to examine in detail the anatomy of one species, *Platypleura capitata* (Oliv.), on which most of the experiments were performed. Fig. 1 (which is the same as text-fig 2 of that paper apart from slight corrections and alterations to the lettering) displays this anatomy as seen from within in a specimen bisected just to the left of the mid-line. The important muscles for sound-production are the tymbal muscle (here shown cut away), which is directly responsible for the buckling of the tymbal and the emission of pulses of sound, the tensor muscle (*tens. m.*), which increases the curvature of the tymbal and so increases the volume of emitted sound, the dorsal muscles (*d. m.*), possibly tensor in function but also serving to raise the abdomen in antagonism with the ventral muscles (*vent. m.*), and the abdominal muscles (*dors. abd. m.*, *lat. abd. m.*, *vent. abd. m.*) which compress or expand the abdomen and with it the resonant tracheal air sacs. Indirectly connected with sound-production is the detensor muscle (*det. m.*), which creases the (auditory) tympanic membrane before sound-emission starts and so protects it from damage.

In the earlier paper some suggestions were made about the homology of these muscles and of the skeletal structures to which they are attached, and the original drawing of the anatomy was lettered in accord with these homologies. It has now become clear that *Platypleura* is a genus of cicada which has become modified from the basic Auchenorrhynchous plan further almost than any other, and that some of the arguments based on the anatomy of this genus are liable to be misleading. It is known from the work of Ossiannilsson (1949) that sound is produced, by a mechanism similar to that of cicadas, by many of the smaller Homoptera Auchenorrhyncha, and there is therefore a problem in comparative anatomy to relate the state of affairs found in cicadas to the basic plan which seems to be followed in the rest of the sub-order.

Myers (1928), who made a notable contribution to knowledge of the Cicadidae, was of the opinion that within this family there was (with one notable exception) only a slight variation of anatomical plan. A warning not to accept too readily this supposed uniformity is provided by Hagiwara's evidence (Hagiwara, Uchiyama, and Watanabe, 1954) that an essential part of the physiological mechanism described by Pringle (1954) for *Platypleura capitata* is not present in *Meimuna opalifera* and a number of other species, though it is found in *Platypleura kaempferi* ; some anatomical differences between different cicada genera will be described later.

But of paramount importance in relating cicadas to the other Auchenorrhyncha is Myer's exception, the genus *Tettigarcta*. The two species of this genus, *tomentosa* White and *crinita* Distant are found in the mountains of, respectively, Tasmania and New South Wales, always at a considerable altitude. The anatomy of *T. tomentosa* has been partially described by Evans (1940), who also discussed its status as a Tertiary relic. Myers (1928), who knew it only from poorly preserved material, emphasized the primitiveness of the genus, and Evans added to the evidence for this view. A few well-preserved specimens have now made it possible to extend our knowledge of this important " missing link " in regard, particularly, to the organs of sound production and reception.

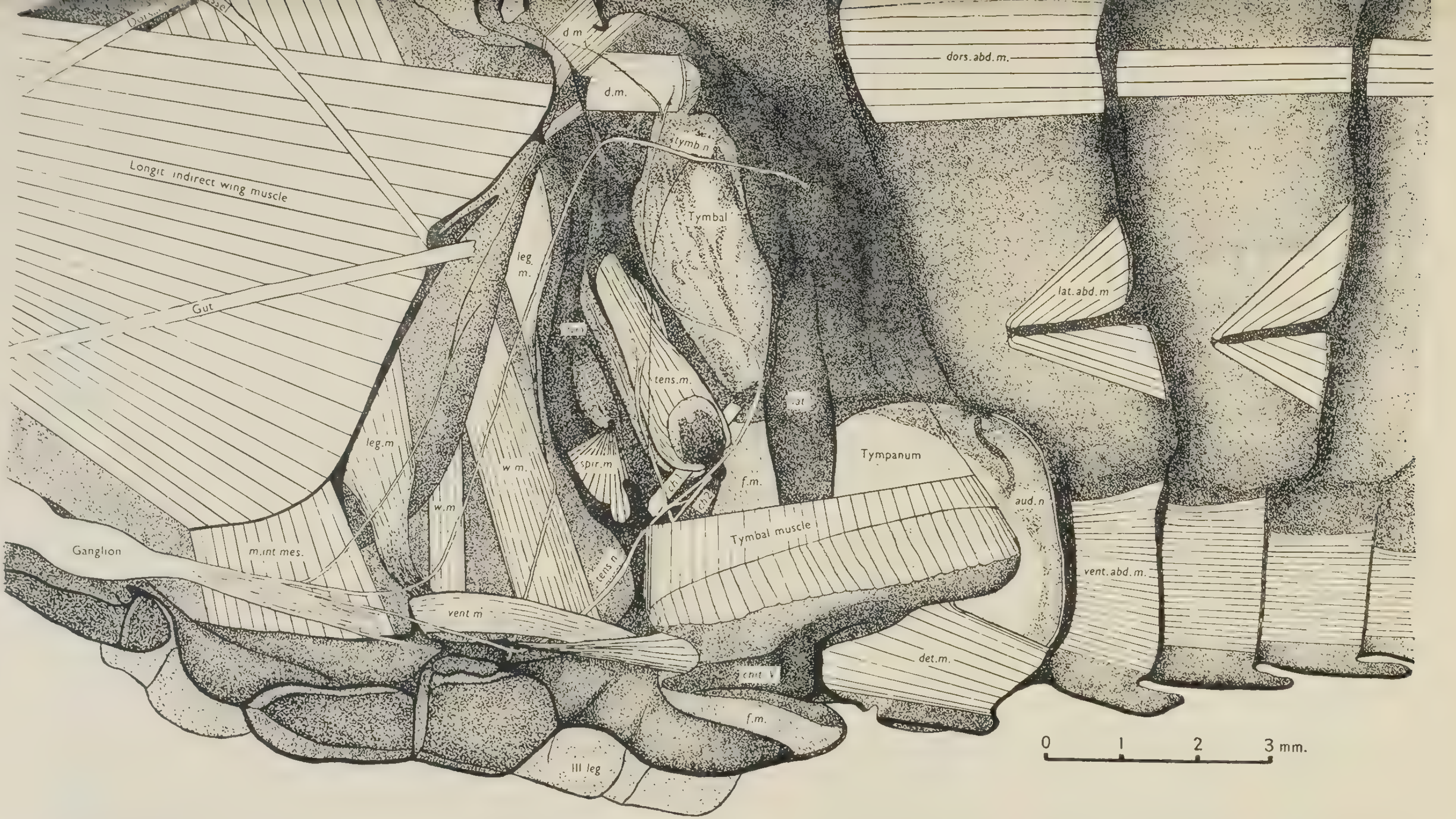


FIG. 1.—The muscles and nerves concerned in sound-production and reception in *Platypleura capitata* (Oliv.) (Cicadidae). Apart from the thoracic ganglion, gut, blood vessel and the base of the chitinous V, which are shown intact, the remaining structures are duplicated on the left side of the body. The tymbal muscle has been cut across near its base and the abdominal, auditory and leg nerves are cut near the ganglion. The operculum is not drawn. *chit. V*, base of chitinous V; *ch.*1, *ch.*2, chordotonal organs 1 and 2; *f.m.*, folded membrane; *lat.*, lateral arm of chitinous V; III *leg*, metathoracic leg. Muscles: *d.m.*, dorsal muscles; *det.m.*, detensor tympani muscle; *dors.abd.m.*, dorsal longitudinal abdominal muscles; *dvm.*, dorso-ventral muscle; *leg.m.*, metathoracic leg muscles; *m.int.mes.*, musculus intersegmentalis mesothoracicus; *spir.m.*, spiracular muscle; *tens.m.*, tensor muscle; *vent.abd.m.*, ventral longitudinal abdominal muscles; *vent.m.*, ventral longitudinal muscle of metathorax; *w.m.*, metathoracic direct wing muscles. Nerves: *aud.n.*, auditory nerve; *tens.n.*, tensor nerve; *tymb.n*, tymbal nerve.

One of the objectives in a comparative anatomical study is the formulation of a plausible phylogenesis, with continuity of useful function. Evidence is needed on the question how the Auchenorrhyncha evolved a mechanism of inter-sexual sound signalling which is basically different from that found anywhere else in the animal kingdom.

RESULTS.

Jassidomorpha.

The Jassidomorpha of Evans (1945) include the Cercopoidea and Jassoidae in the more recent classification of Brues, Melander and Carpenter (1954). In these groups and in the Araeopidae of the Fulgoromorpha Ossiannilsson (1949) has described, for a large number of species, the anatomy of the musculature of the anterior abdominal segments and the audible characteristics of the song. In many genera " the first abdominal dorsum contains laterally a convex, hyaline and thin but well sclerotized, elastic surface adorned by a number of parallel or concentric lines of deviating refraction ". This is the ' striated tymbal ', without doubt homologous with that of cicadas ; in species where it is absent there may, nevertheless, be " a system of strengthened inner lists and often clump-shaped sclerites in the same region and sometimes in the adjacent part of the second abdominal tergum, too." In many species both sexes have this specialized structure ; in others it is better developed in the male and in some in the female.

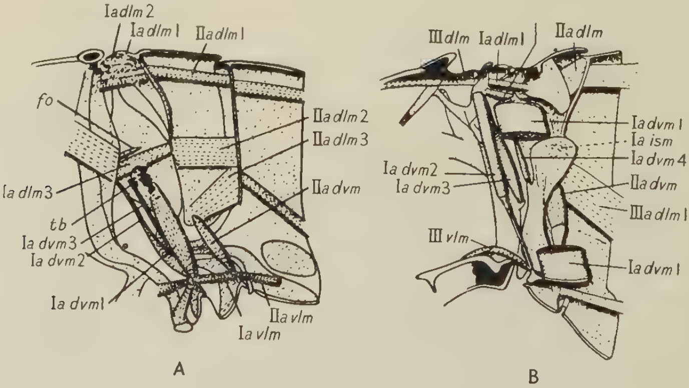


FIG. 2.
A. *Neophilaenus campestris* (Fall.), male.
B. *Aphrodes bicinctus* (Schrnk.), male.
Right half of hind part of metathorax and base of abdomen from the inside. III metathorax ; *Ia, IIa, IIIa,* 1st, 2nd, 3rd abdominal segments ; *dlm,* dorsal longitudinal muscle ; *dvm,* dorso-ventra muscle ; *ism,* intersegmental muscle ; *vlm,* ventral longitudinal muscle ; *fo,* internal strengthening of tergal plate ; *tb,* striated tymbal. (From Ossiannilsson, 1949.)

Fig. 2 reproduces from Ossiannilsson (1949) the anatomy of a male Cercopid and a male Euscelid (Jassoidae), and his description follows. In the Cercopid there is a clearly striated tymbal about half-way up the first abdominal tergum, and a muscle ($Ia\ dvm_1$) attached from it to the first abdominal sternum. Muscles $Ia\ dvm_2$ and $Ia\ dvm_3$ also run from the first abdominal sternum to the region immediately anterior to the tymbal. In the Euscelid there is no striated tymbal, but a large muscle $Ia\ dvm_1$ running from the first abdominal sternum to a modified region of the first abdominal dorsum, and a complicated set of dorso-ventral muscles in the segment, labelled $Ia\ dvm_2$, $Ia\ dvm_3$ and $Ia\ dvm_4$.

Ossiannilsson is able to conclude that the muscle which he calls $Ia\ dvm_1$ is the main sound-producing muscle in all genera except *Paropia* and *Cicadella* ;

he correlates its size and development in the two sexes with their respective powers of sound-production, and he homologizes it with the tymbal muscle of cicadas. For muscle *Ia* dvm_2 he suggests a number of possible functions, including that of changing " conditions of tension in the tergal membrane " and of producing " modifications in the quality of sound " ; also that it may be responsible for changes in the frequency of the sound by altering the resting length of muscle *Ia* dvm_1 ; in this role he suggests that it is antagonistic to the ventral longitudinal muscles of the metathorax and first abdominal segments. These functions are very similar to those demonstrated by Pringle (1954) for the tensor muscle of cicadas, which lies in a similar morphological position. Functional evidence of the existence of tensor muscles in Cercopids and Jassids was obtained by Ossiannilsson from the variations in amplitude and pitch of the song. An oscillogram of the alarm call of a male Jassoid Homopteran, *Aphrodes nervosus*, is shown in fig. 3 ; the variation in amplitude of the song (particularly in the amplitude of the first pulse of the pair produced by the IN-OUT click of the tymbal ; Pringle 1954) again strongly suggests that a tensor muscle is present, functioning in much the same way as that of cicadas. The detailed homologies of the various dorso-ventral muscles other than *Ia* dvm_1 will be discussed later.

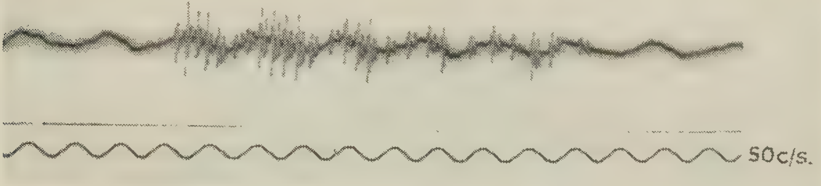


FIG. 3.—Oscillogram of the alarm call of a male *Aphrodes nervosus* recorded with the insect lightly affixed to a wire held in the needle-holder of a piezo-electric gramophone pick-up.

Tettigarcta.

Evans (1940), in his description of the anatomy of *Tettigarcta tomentosa*, identifies the tymbals and tymbal muscles in both sexes but regards them as non-functional relics of well-developed sound-producing organs in an early cicadan stock from which this genus is descended. He finds no trace of auditory organs in either sex of *Tettigarcta* in spite of a slight difference in consistency of second abdominal sternite in the region the tympanum " would occupy if present ", and concludes that these structures also have degenerated when the sound-organs lost their power to function.

In the present investigation careful dissections have been made of a male *T. tomentosa* and a female *T. crinita*, and the salient points checked in the other sex of each species ; there are no differences between the two species which are significant for the present problem.

Fig. 4 shows the general appearance of the musculature of the male *T. tomentosa* as seen from within, in a specimen bisected vertically in the mid-line. The very large pronotal shield was remarked upon by Myers (1938) ; Evans (1940) points out that this condition is common in the Homoptera except in the Cicadidae. The mesothorax has a similar, scutellar-like enlargement which covers the metathorax and the first two abdominal segments. Another feature of interest is the separateness of the three thoracic ganglia, the abdominal ganglia being fused with the third thoracic; this is a more primitive arrangement of the nervous system than is found in any other Homopteran.

The musculature of the metathorax is very similar to that of a true cicada (*cf.* fig. 1). The ' musculus intersegmentalis mesothoracicus ' (Weber, 1928) is well-developed as a basal anchorage for the large phragmata which form the posterior attachment of the longitudinal wing muscles; the wing and leg musculature of the metathorax resembles that of *Platypleura*, and there are similar ventral muscles.

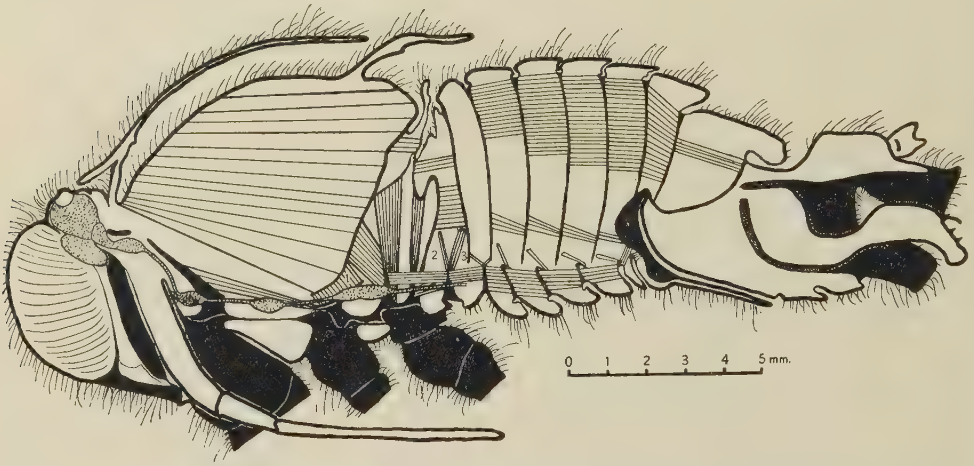


FIG. 4.—*Tettigarcta tomentosa*, male. Outline drawing of the right half of the insect seen from the inside; only in the metathorax and in the first six abdominal segments has care been taken to draw all the somatic muscles. 1, ' musculus intersegmentalis mesothoracicus '; 2, tensor muscle; 3, tymbal muscle.

The muscles and nerves in the ventral part of the metathorax and abdomen are shown in more detail in fig. 5, which also shows the striated tymbal and the positions of the spiracles. The following points are noteworthy :—

(1) The tymbal muscle is innervated, as in true cicadas, by a nerve which runs median to the ventral muscle and also sends a fibre to the spiracle lying in the metathorax.

(2) The tensor muscle complex is innervated from a nerve which, as in true cicadas, runs lateral to the ventral muscle. In *Tettigarcta* it appears to form a diffuse complex with the tymbal nerve at one point, but the fibres composing this complex could not be traced. Part of the tensor is inserted basally near the basal attachment of the tymbal muscle, and part on a detached sclerite.

(3) Two elongated chordotonal organs are innervated by the tensor nerve. One of these (ch. 1) runs from the metathorax to the rim of the tymbal, the other (ch. 2) from lower on the metathorax to the detached sclerite.

(4) There is a definite ' folded membrane ' in the same position as that of true cicadas suggesting movement of the basal tymbal muscle attachment relative to the thorax. There are no abdominal air sacs similar to those of true cicadas, and no lateral abdominal muscles arranged to extend the abdomen; the small lateral intersegmental muscles in the abdomen appear to be incapable of producing more than a very small movement of this type.

(5) There is a slender dorso-ventral muscle in the metathorax.

(6) There is no dorsal longitudinal musculature in the abdominal segment behind that containing the tymbal muscle (fig. 4).

The condition in the female is shown in fig. 6, from which nerves are omitted. The striation of the tymbal is much less marked in this sex, and the tymbal muscle is smaller. Slender dorso-ventral muscle strands occur in the metathorax and in each abdominal segment spanning the body cavity, and there are definite, though much reduced muscle strands representing the dorsal longitudinal musculature of the second abdominal segment. Otherwise the muscular anatomy is very similar to that of the male.

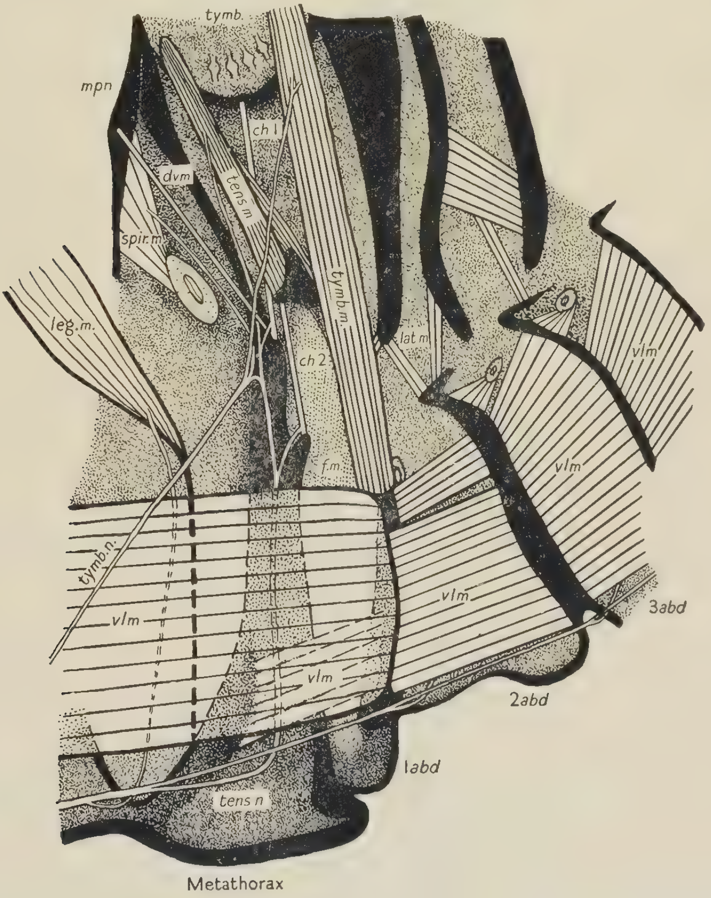


FIG. 5.—*Tettigarcta tomentosa*, male. Detail of muscles and nerves in the ventral part of the metathorax and abdomen. *ch*.1, *ch*.2, chordotonal organs 1 and 2 ; *f.m.*, folded membrane ; *mpn*, metapostnotum ; *tymb.*, striated tymbal. 1*abd*, 2*abd*, 3*abd*, abdominal segments. Muscles : *dvm*, dorso-ventral muscle ; *lat.m.*, lateral abdominal muscles ; *leg.m.*, metathoracic leg muscle ; *spir.m.*, spiracular muscle ; *tens.m.*, tensor muscle ; *tymb.m.*, tymbal muscle ; *vlm*, ventral longitudinal muscles. Nerves : *tens.n.*, tensor nerve ; *tymb.n.*, tymbal nerve.

The lower part of the first three abdominal segments of the male is shown again in fig. 7, after removal of the ventral longitudinal muscle of the segment behind the tymbal muscle. Lateral to this muscle, and in a position comparable to that of the auditory organ of true cicadas, is a pair of chordotonal organs innervated by a stout branch of the segmental nerve. The anterior edge of the sclerite is indented in this region so that the vertical chordotonal organ spans a thin region of the cuticle. The longitudinal organ is fan-shaped, the sensilla

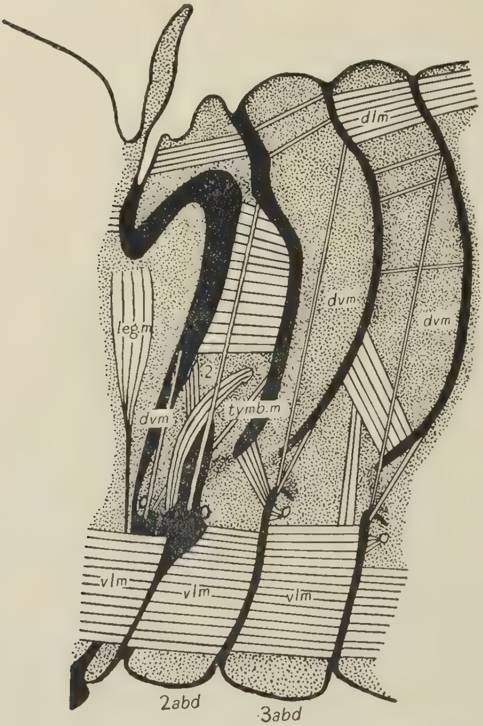


FIG. 6.—*Tettigarcta crinita*, female. Detail of muscles. *dlm*, dorsal longitudinal muscle; 2, tensor muscle; other lettering as in Fig. 5.

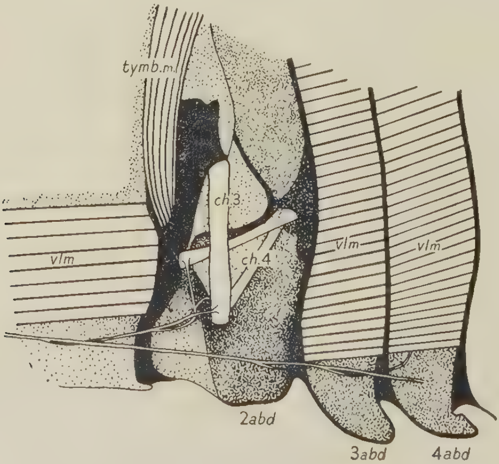


FIG. 7.—*Tettigarcta tomentosa*, male. Ventral part of base of abdomen, with the ventral longitudinal muscle of the second abdominal segment removed. Lettering as in Fig. 5; *ch*.3, *ch*.4, chordotonal organs 3 and 4.

converging to a point on the side of the abdomen which corresponds in position with the auditory capsule of true cicadas. The indentation and the swelling in the position of the auditory capsule were figured by Evans (1940) in external view only and he therefore did not find the chordotonal sensilla.

Cicadidae (other than *Tettigarcta*).

The morphology of the metathorax and first two abdominal segments in male Cicadidae is greatly influenced by the enormous development of the tymbals and tymbal muscles. These muscles are attached basally to the strongly sclerotized structure known as the 'chitinous V' (fig. 1), whose origin and homology has been the main problem in cicada anatomy since the time of Reamur (1740).

A full review of the literature on the subject is given by Myers (1928, 1929). He points out that although the chitinous V appears to be an endoskeletal structure, it is, in fact, part of the external surface of the insect which has become depressed and thickened; the normal plane of the venter is defined by the covering operculum, a projecting fold of the metathoracic exoskeleton.

Seen from the outside this depressing of the cuticle produces on each side of the body a wide vertical groove (fig. 8) which is divided into dorso-lateral and ventro-lateral portions by a horizontal ridge projecting forwards from the lateral angle of the abdomen. In the ventral half the forward-facing surface of the groove forms the tympanum, the backward-facing surface the folded membrane (which allows the abdomen to move relative to the thorax); the base of the groove is strongly sclerotized and forms the lateral arm of the chitinous V, which is the compression member balancing the tension in the tymbal muscle. In the dorsal half the forward-facing surface of the groove is strongly sclerotized, and the backward-facing surface is the tymbal.

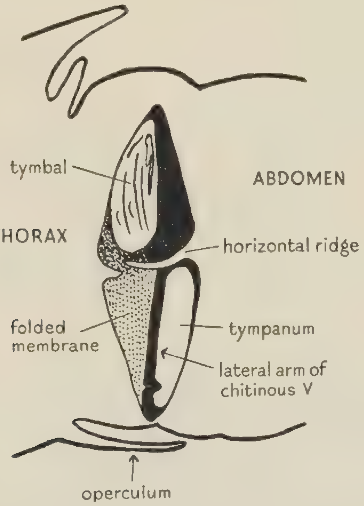


FIG. 8.—Diagram to explain the anatomy of the tymbal and associated structures in a cicada.

Myers (1928) also remarks on another feature which has greatly complicated the anatomy of some cicadas including *Platypleura*. In *Tibicina septemdecim* (which may in this respect be regarded as one of the more primitive cicadas) the sclerotized base of the ventro-lateral groove (the chitinous V) is buckled inwards near the mid-ventral line; this has been shown as a kink in the diagram of fig. 8. In transverse section it takes the form shown diagrammatically on fig. 9 *b*. This buckling increases the area of basal attachment of the tymbal muscles. Myers remarks that in *Tibicen chloromera* the longitudinal ridges so formed are better developed and practically meet; in *Platypleura* they not only meet and fuse in the mid-line (fig. 9 *c*) but are prolonged forward and backwards as an internal skeleton to provide a much increased area of attachment for the tymbal muscles. By the fusion of the internal ridges a narrow canal is formed in the mid-ventral line in which run the nerve fibres supplying all structures posterior to this point.

In *Platypleura* (fig. 1) the strong base of the ventral part of the depressed groove (the chitinous V) is firmly anchored to the strong forward-facing surface of the dorsal part of the groove, completing a rigid strut supporting the tymbal muscle. This condition seems to be the most advanced stage of development of the sound-production system; in some cicadas (for example, *Huechys incarnata* described by Vogel, 1932) the apex of the groove is tied to the dorsum by a tensor tympani muscle. Fig. 10 shows outline drawings of the tympanum in three genera. When it is borne in mind that the tensor tympani is present in the freshly emerged male even of *Platypleura* (Pringle, 1954) it seems clear that the presence or absence of this muscle in any given adult genus is of little anatomical significance.

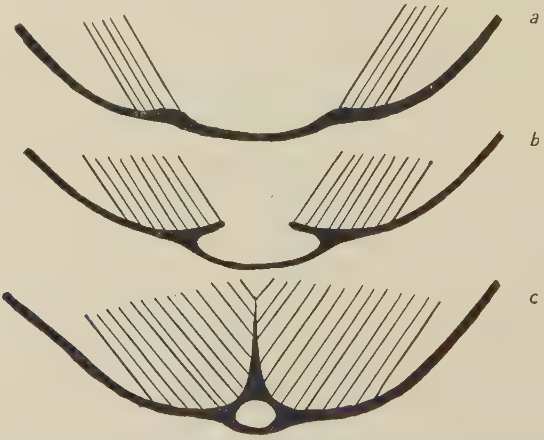
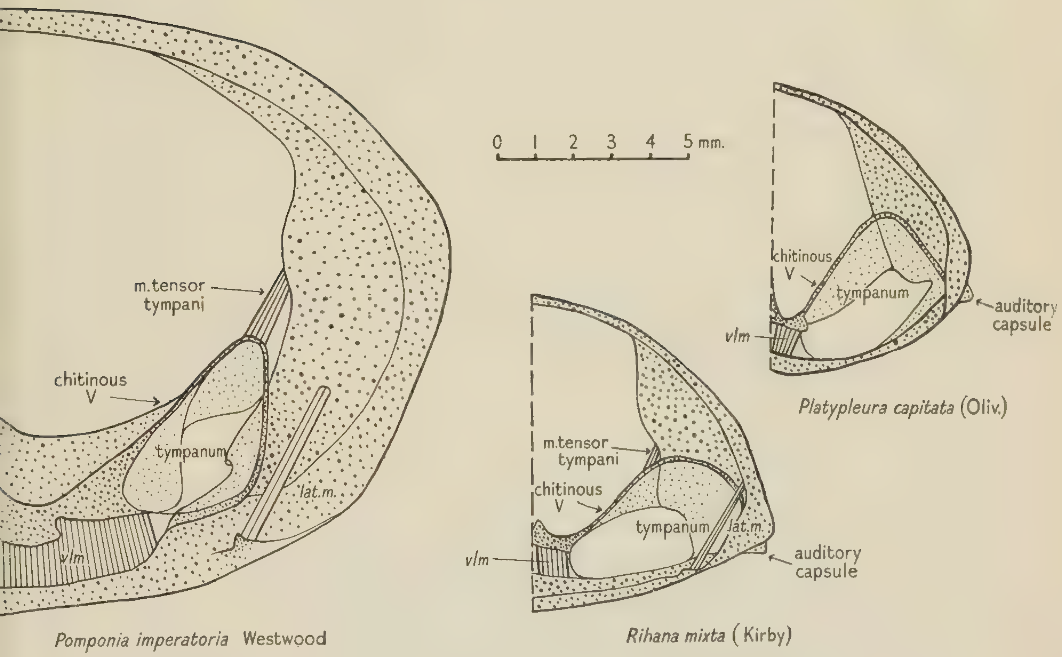


FIG. 9.—Diagrams of the structure of the ventral sclerite to which the tymbal muscle attaches in cicadas, as seen in transverse section. *a*, primitive condition; *b*, intermediate condition found in some cicadas; *c*, condition in *Platypleura*.

This picture of the actual anatomy of the Cicadidae is now clear. It is, however, by no means easy on this picture to draw lines of demarcation between the thorax and the first abdominal segments, and it is to settle this question that Myers turns to an examination of the female and the last instar nymphs. Fig. 11 shows the anatomy of the female *Platypleura*. There is no sign of a tymbal muscle or of any homologue of it. The tensor muscle is very similar to that of the male and has a single associated chordotonal organ; a thin dorso-ventral muscle is present at the hind margin of the metathorax as in the male. The tympanum is well-developed, though smaller than in the male, and there is a tensor tympani muscle; a few fibres of a lateral abdominal muscle can be found immediately behind the tympanum. As in the male there is one segment devoid of dorsal longitudinal muscle, and in the female the ventral longitudinal muscle is also missing in the same segment. A strong auditory nerve runs to the auditory capsule and a branch innervates a second small chordotonal organ in the same position as that of *Tettigarcta*. Other muscles are present as in the male.



Pomponia imperatoria Westwood

Rihana mixta (Kirby)

Platypleura capitata (Oliv.)

FIG. 10.—Outline drawings of tympanum and associated structures in three species of cicada. *vlm*, ventral longitudinal muscle (detensor tympani muscle); *lat. m.*, lateral abdominal muscle.

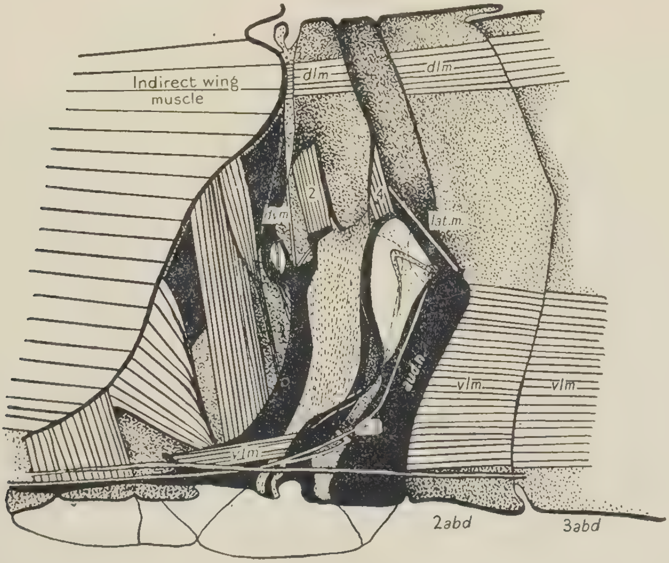


FIG. 11.—*Platypleura capitata*, female. Detail of muscles and some nerves in the metathorax. *aud.n.*, auditory nerve; 2, tensor muscle; 4, tensor tympani muscle; other lettering as in figs. 5, 6 and 7.

Myers (1928) had available nymphs of three species of *Melampsalta* and of *Tibicina septemdecim*, but he gives only a brief description of the anatomy of either sex ; " the male ultimate nymph shows surprisingly little difference from the female condition ". Well-preserved but unidentified specimens of last-instar nymphs have been examined in the course of the present investigation and Myers' remarks are not fully substantiated. Fig. 12 shows a male last-instar nymph from Brazil. The tymbal and tensor muscles are beginning to develop, and (here confirming Myers) " there is a raised dome-like area of smooth, white, very thin skin where the tymbal will lie . . . ." The narrow dorso-ventral muscle strands in the metathorax and in each abdominal segment resemble those found in the female *Tettigarcta*, and it is interesting to see how the strand attached near the base of the tymbal muscle appears to be pulling in the ventro-lateral cuticle in a manner very similar to the tensor tympani muscle. Dorsal and ventral longitudinal muscles are present in each segment. There is a chordotonal organ in the second abdominal segment in the same position as that of *Tettigarcta* and the female *Platypleura* adult.

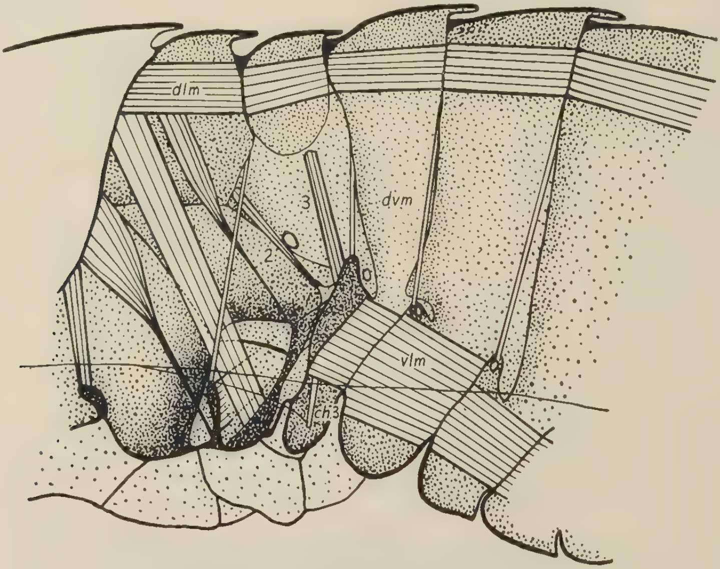


FIG. 12.—Unidentified male cicada last instar nymph from Brazil ; details of muscles in metathorax and abdomen. 2, tensor muscle ; 3, tymbal muscle ; other lettering as in Figs. 5, 6 and 7.

DISCUSSION.

The production of sound pulses by the sudden buckling of a portion of the exoskeleton is a method not found in any groups of insects other than the Homoptera Auchenorrhyncha. Within this group there is, in spite of considerable difference in general appearance, such a close similarity in the basic plan that it would be unreasonable to suppose that the technique has evolved twice.

Morphology.

All recent authors who have described these insects are agreed that the sound-production organ is a development of the first abdominal segment ; this is certainly the obvious conclusion to draw from an examination of a Cercopid, Jassid or of *Tettigarcta*. On the other hand, as was pointed out in an earlier paper (Pringle, 1954) the innervation of the tymbal muscle in cicadas (and in *Tettigarcta*) suggests that this is a metathoracic muscle which has migrated in a posterior direction. Neither in cicadas, in *Tettigarcta*, nor in Cercopids and Jassids is there any indirect flight musculature in the metathorax, all the power for movement of the hind wings being transmitted by wing-coupling from the front pair (Pringle, 1954, for *Platypleura* ; anatomical evidence in the other groups) ; the slender dorso-ventral muscle in the metathorax has no connection with the movement of the wings. It was also suggested in the earlier paper that the occurrence of a myogenic rhythm in the cicada tymbal muscle was evidence in favour of the view that this is a modified wing muscle, since this property has otherwise been described only for indirect flight muscles (Pringle, 1949 ; Roeder, 1951) ; but the existence of cicada genera in which the tymbal muscle does not possess this property (Hagiwara, Uchiyama and Watanabe, 1954) removes the weight from this argument, and suggests that the myogenic rhythm has evolved more than once.

The morphological problem should be capable of solution from a study of the nymphal and female conditions and from the location of other structures in the region of the first abdominal segment. Unfortunately neither approach yields conclusive evidence from a study of cicadas alone. In the cicada nymph (fig. 12) the segmental boundaries are ill-defined. Dorsally there is a complete series of longitudinal muscles which define the segments, but the first abdominal dorsum has only a small sclerotized region which does not reach down to the point of attachment of the tymbal muscle. Ventrally the tymbal muscle is attached to a sclerite from which run, forward, two longitudinal muscles to the furca of the metathorax and to the posterior region of metathorax, and, backward, a longitudinal muscle to the anterior edge of the third abdominal segment. The sclerite therefore lies in the region between the posterior border of the metathorax and the anterior border of the second abdominal segment, but it is not possible to say which segment bears the origin of the tymbal muscle.

In the female cicada (fig. 11) the complete absence of any sign of the tymbal muscle is remarkable. A ventral sclerite homologous with the base of the chitinous V of the male can, however, be identified by its relation to the tympanic membrane ; a tensor tympani muscle, apparently formed from one of the dorso-ventral muscle strands of the nymph, pulls in the upper end of this sclerite as in the male. This arrangement locates the sclerite at the boundary of the first and second abdominal segments and the tympanum wholly in the second (*contra* Myers, 1928) ; it is possible that the double appearance of the sclerite in the female indicates the segmental boundary.

Segmental limits should be definable from the position of the spiracles, but in cicadas the spiracles are hard to assign to segments. In addition to one between the prothorax and mesothorax, and one between the mesothorax and metathorax, there is a spiracle of thoracic structure situated apparently on the metathorax. This is the spiracle from which the large abdominal air sacs of the male cicada are supplied, and it also supplies the tymbal muscle. To preserve the segmental series Myers (1928) has to regard this as the first abdominal spiracle migrated forwards to the metathorax and the spiracle situated near the tympanic membrane as the second abdominal migrated forward to the first abdominal segment. If, as has been suggested above, the tympanum lies wholly in the second abdominal segment, its spiracle ceases to be a problem ; Ossiannilsson perhaps provides the clue to the other, for he suggests that an apparently similar situation in Cercopids is due to the presence of a large metapostnotum—a part of the first abdominal segment firmly attached to the metathorax.

Turning now to *Tettigarcta* we find an interesting intermediate condition between that found in the Cercopids and in the true cicadas ; in many respects this genus makes it easier to understand the segmentation problem. Fig. 5, showing the muscles of the male in detail, should be compared first with fig. 2 A of the Cercopid, *Neophilaenus campestris*. In this species Ossiannilsson identifies four dorso-ventral muscles arising from the first abdominal sternum. Muscle $Ia\ dvm_1$, running to the posterior edge of the striated tymbal, is clearly homologous with the tymbal muscle. Muscles $Ia\ dvm_2$ and $Ia\ dvm_3$ run to the hind border of the metapostnotum in front of the tymbal and seem to correspond to the two parts of the tensor muscle of *Tettigarcta* ; muscle $Ia\ dvm_4$, which in *Neophilaenus* " attaches itself by both ends to membranous parts of the body wall near the fourth spiracle " is not shown on his figure. There is thus a close similarity with *Tettigarcta* in regard to dorso-ventral muscles apart from the fact that in that genus the larger part of the tensor muscle is attached basally to a detached sclerite and not directly to the same sclerite from which arises the tymbal muscle. There is, however, a difference between Ossiannilsson's account and the condition in *Tettigarcta* in regard to the ventral longitudinal muscles. As in *Tettigarcta, Neophilaenus* has two muscles running forward from the basal sclerite of the tymbal muscle (fig. 2 A). One of these is shown attaching to the posterior edge of the metathorax ; the anterior insertion of the other is not included in the figure but it presumably goes to the metathoracic furca. From the sclerite backward there runs a single ventral longitudinal muscle which Ossiannilsson labels *Ia vlm* ; *Tettigarcta* has a similar muscle, but a count of the segments behind this point reveals that it is the muscle of the second abdominal segment and not of the first, being inserted posteriorly on the anterior edge of the third abdominal sternum. The double nature of the longitudinal muscle running forward from the chitinous V is also shown in fig. 1 in the cicada *Platypleura*, and it seems only possible to conclude that the lower of these two is the ventral longitudinal muscle of the first abdominal segment, whose anterior edge is firmly united with the metathorax as is the metapostnotum in the dorsal region. On this view the folded membrane is part of the first abdominal segment rather than intersegmental, and, once again, the chitinous V and the sclerite to which the tymbal muscle is attached in *Tettigarcta* and in Cercopids must lie at the boundary of the first and second segments.

Now comparing *Tettigarcta* with *Platypleura* (figs. 5 and 1) the only difficulty concerns the tensor muscle, which arises in *Platypleura* from a peg firmly attached to the metathorax, instead of from a detached sclerite in *Tettigarcta*. The identity of the two points is shown by the chordotonal organs. In both genera one of these runs from the metathorax to the lower tymbal rim, but is thickened in *Platypleura* to form an elastic ligament possibly without sensory function ; it was labelled as such by Pringle (1954). The other in *Tettigarcta* joins the detached sclerite to the metathoracic edge and in *Platypleura* runs from the peg to a point lower on the metathorax. This migration of the base of the tensor muscle seems to be yet another piece of evidence for the tendency of the anterior edge of the first abdominal segment to become attached to the metathorax.

Although a final judgment on the segmental origin of the tymbal muscle and chitinous V of cicadas must probably await a study of a full series of developing last instar nymphs, the weight of evidence adduced here tends to reinforce the view that they are first abdominal structures, with the anterior edge of the second abdominal segment contributing to the sternal sclerite. The tymbal muscle is probably a dorso-ventral muscle, but seems to be a unique development of the first abdominal segment. Fig. 6 of the *Tettigarcta* female and fig. 12 of the male cicada nymph show that the slender dorso-ventral strands which occur in these insects differ considerably from the tymbal muscle in their points of insertion and form a complete segmental series without it ; the muscle apparently situated at the hind border of the metathorax inserts directly in the metapostnotum and is to be regarded as lying at the anterior edge of the first abdominal segment. Equally clearly the tymbal muscle does not form part of the series of lateral muscles. Its innervation by a nerve which runs median to the ventral longitudinal muscle may be thought to be consistent with the view that it is a dorso-ventral muscle since this is the course taken by the nerves to the indirect flight muscles in the metathorax ; but perhaps too little is known about the rules governing the course of nerve fibres in insects for it to be right to give much weight to this piece of evidence.

Continuity of function.

The efficient generation of airborne sound demands in the mechanism a structure which is mechanically resonant at the frequency involved. The maximum frequency at which muscles can contract is of the order of 100/sec. for normal excitatory processes, and up to about 1000 sec. for small muscles with a myogenic rhythm. Structures which are mechanically resonant at these frequencies are possible only for large or very large insects. The more efficient method is therefore adopted by some of the Auchenorrhyncha of producing pulses of high-frequency sound, the pulses corresponding to contractions of the muscle and the high-frequency to the resonance of the mechanical structures involved. To excite into oscillation a high-frequency resonator a very rapid transient impulse is needed, and this is achieved through a click mechanism in a portion of the exoskeleton whereby energy stored during muscular contraction in the elasticity of the cuticle is suddenly dissipated.

The reception of airborne sound is most efficiently achieved by means of a tympanic membrane which matches the density of the air to that of the receptor organ. The cicada ear (like all insect auditory organs) demodulates the received sound, delivering to the central nervous system impulses which correspond to the pulses received ; the high-frequency sound acts as a carrier wave for information contained in the pulse train.

In the Cercopids, Jassids and *Tettigarcta* there is no resonant air sac or tympanic membrane, but there is a click mechanism in the striated tymbal and a system of chordotonal organs on the receiver side. This mechanism could be a very efficient sender and receiver of vibration in the form of pulse transients transmitted through solid objects, but will be inefficient for airborne sound and could be expected to function in this way only over very short distances. It is therefore easy to see how a great advantage would be gained by the true cicadas with their air sacs and tympana over an insect like *Tettigarcta*, and since the airborne sound is functioning merely as a carrier wave no new nervous mechanism would be needed for this lengthening of the transmission channel.

It is much more difficult, however, to make suggestions about the early stages in the evolution of the mechanism. Were it possible to substantiate from comparative anatomical evidence the view that the tymbal system derives from the mechanism of flight no difficulties would arise ; for responses to the flight tone have been demonstrated in other insect groups (mosquitos; Roth, 1948), and the absence of power-producing flight muscles in the metathorax suggests a gradual transition from an effectively four-winged to an effectively two-winged insect, with the sound-production system gradually separating from that of flight. The link which *Tettigarcta* provides between the true cicadas and the other Auchenorrhyncha must, however, dispose of this suggestion, which would in any case meet with a difficulty in the absence of an efficient mechanism for the production and reception of airborne sound in the Cercopids and Jassids.

Two alternative views seem possible. One would regard the development of a dorso-ventral muscle in the first abdominal segment as a case of the serial repetition of a segmental structure extending in this group of insects one segment further back than in the majority, the click mechanism in the tergal region being a parallel development to that of the wing articulation. The functional advantage of a method of attracting the sexes to each other might be thought to be sufficient to preserve and encourage such an ontogenetic tendency ; it does not seem possible in this way, however, to explain the location of the receptor on the second abdominal sternum, and the fact that there is no similar tendency in other groups of insects inevitably weakens the argument.

The other view, which is put forward in the hope that it may perhaps stimulate thought on the evolution of patterns of intersexual activity and behaviour, is based on the idea that display actions derive originally from movements made during copulation. In the modern concepts of ethology both display movements and actual copulatory movements are to be regarded as appetitive actions necessary before the releaser situation is reached for the final consummatory act. In a performance in which action (or unwonted inaction) by both partners is required to produce the pattern of successive releasers for further action, it is to be expected that in the course of evolution there will be a change in the nature of the reactions and releasers when this can lead to a more rapid or more efficient performance of the consummatory act. If a movement which is originally effective in stimulating the sexual partner only during copulation can evolve into one which produces the correct behaviour at a distance, it is likely to be preserved by natural selection.

A possible reason for the development of the vibration-producing organ on the first abdominal dorsum and the vibration-receiving organ on the second abdominal sternum may be that these regions came into contact during copulation. If the male mounts the female, then the primitive direction of useful transmission must have been from female to male, but since the evidence suggests that the primitive condition is a similar development in both sexes this may have been enough to start the evolution of the structures in these locations. Only by actual contact could small movements be effective, and small movements of the cuticle must have preceded rapid click movements unless the click mechanism evolved for some other purpose. Once the production and reception of vibration had become established as an intersexual stimulus during copulation, it is not difficult to see how it might have extended to provide a means of attraction between the sexes as a prelude to copulation. At this stage the greater development of the sound-production organ of the male may have started in many species : a development carried to its limit in true cicadas, the females of which are perhaps silent because the great enlargment of the air sacs is inconsistent with the production of large numbers of eggs.

Acknowledgments

I am very grateful to Professor V. V. Hickman and Dr. A. J. Nicholson for arranging to send me well-preserved specimens of *Tettigarcta tomentosa* and *T. crinita.*, and to Dr. W. E. China for the loan of specimens from the British Museum (Natural History).

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Summary.

(1) An account is given of the anatomy of the organs of sound production and reception in *Tettigarcta tomentosa* and *T. crinita*, primitive cicadas from Australia.

(2) This genus provides a link between the Cercopids and true cicadas and makes it possible to suggest detailed homologies for the muscles and other structures concerned in sound-production. It is concluded, contrary to Pringle (1954), that the tymbals and tymbal muscles of cicadas are developments of the first abdominal segment.

(3) The evolution of inter-sexual sound signalling in the Homoptera Auchenorrhyncha is discussed in general terms. It is suggested that the system may have originated from movements made during copulation and evolved through a stage involving pulse vibrations.

CHEMICAL ANALYSIS IN ECOLOGY ILLUSTRATED FROM LAKE DISTRICT TARNS AND LAKES. 1. CHEMICAL ANALYSIS

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(With 3 text-figures.)

Summary.

The major ionic solutes of the surface waters of the English Lake District are the cations—sodium, calcium, magnesium, potassium and hydrogen, and the anions—bicarbonate, chloride, sulphate and nitrate. These ions generally approximate to 99% of the dissolved ionic material. The quantitative chemical differences between the various waters of the district are brought about by the variations in concentration and proportion of these ions. There are two sources of supply of dissolved substances to surface waters: (1) precipitation of air-borne materials, either dissolved in rain or in the form of dry particulate material derived from terrestrial dust or evaporated sea-spray, and (2) direct solution of the rocks and soils of the drainage basin.

Air-borne materials make an important contribution to the dissolved electrolytes of Lake District waters. These materials consist of salts derived from the sea, and of sulphuric acid released into the atmosphere presumably by industrial activities. The composition of the precipitated water therefore approximates to a much diluted sea-water acidified by the addition of considerable quantities of sulphuric acid. This ' primitive ' composition is modified by subsequent additions derived from the rocks and soils, the degree of modification being dependent on the geology of the drainage system.

Geological Outlines of the Area.

The main features of the geology of the district are presented in fig. 1, and are derived largely from Marr (1916) and the simplified geological map of H. H. Thomas contained in that publication. The Lake District is composed of ancient sedimentary rocks of three major types. The northern fells are formed from Skiddaw slate, which is overlain by the Borrowdale volcanic series of rocks. These latter appear at the surface to the north of the Skiddaw slate but more extensively to the south, where they form the fells of the central Lake District. These formations of volcanic ashes, are themselves overlain to the south by a series of somewhat calcareous slates, beginning with a thin

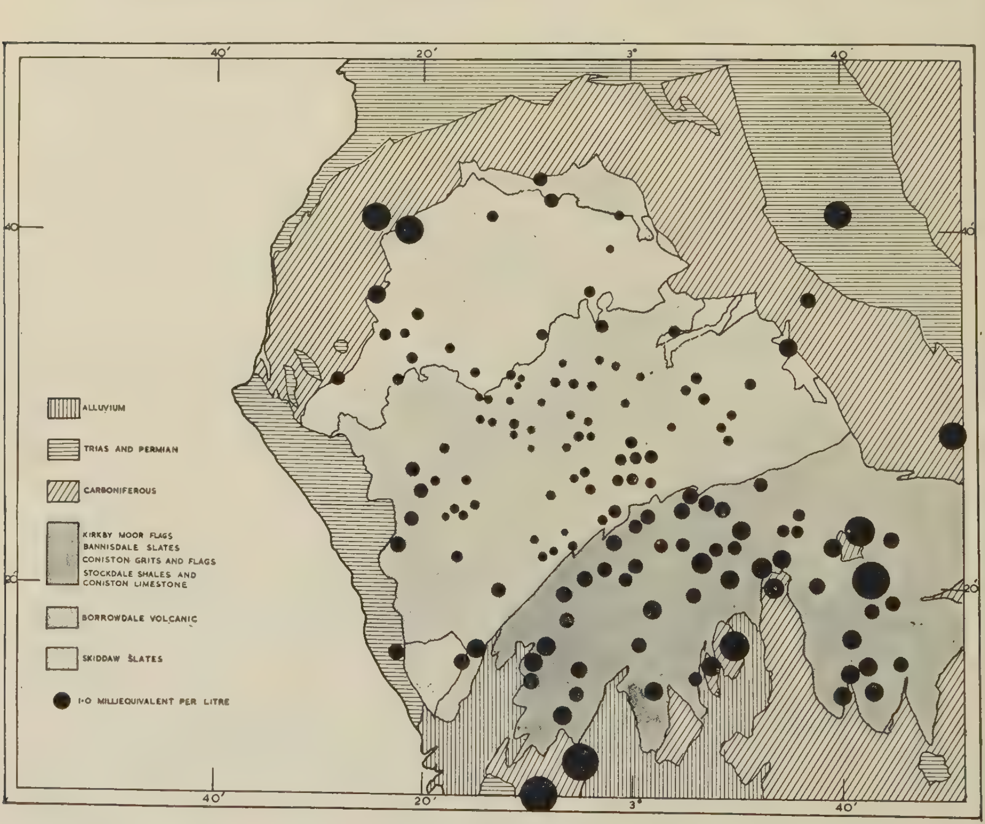

Fig. 1.—Outlines of the geology of the district after H. H. Thomas, and distribution of total ionic concentration in the surface waters. Each circle represents the concentration of ions in a water body.

formation of Coniston limestone and passing into much thicker formations of slates and grits. This central body of Lower Palaeozoic rocks is practically surrounded by formations of Carboniferous and Permian age, the most influential of which from the present viewpoint being the carboniferous limestone.

Distribution of Total Dissolved Ionic Material.

The distribution of the total concentration of dissolved ionic materials is shown in fig. 1 by the black circles superimposed upon the geological outlines. Each circle represents a body of water, large or small. The ionic concentration is expressed in milli-equivalents per litre, the area of the circle being proportional to the concentration. A circle representing 1·0 milli-equivalents per litre is shown for comparison. It will be seen from fig. 1 that the central elevated regions composed of Skiddaw slate and Borrowdale volcanic rocks is characterized by very dilute surface waters with concentrations ranging from 0·15 to 0·3 milli-equivalents per litre. A tendency towards increasing concentrations towards the west of these formations may also be seen and will be discussed later. A marked change in ionic concentration also occurs to the south of the region of Borrowdale volcanic rocks at the junction line between this latter formation and the Coniston limestone—Bannisdale slate series of rocks. Waters whose drainage is influenced by the latter formation have ionic concentrations lying between 0·5 and 2·0 milli-equivalents per litre. A number of water bodies will be seen in fig. 1 lying in or near the periphery of younger Carboniferous rocks, and having very high ionic concentrations, lying between 2·0 and 5·0 milli-equivalents per litre.

The waters of the Lake District may then be divided into three main groups. (1) Central very dilute waters lying on Skiddaw slate or Borrowdale volcanic rocks. (2) Waters receiving much of their drainage from the Coniston limestone —Bannisdale slate formations, and (3) waters lying on the outskirts of the Lake District and influenced by Carboniferous rocks.

These three groups of waters are not only characterized by differences in total concentration of ions, but also by differences in the proportions of the various major ions present in them. The central group (1) waters are dominated by sodium, hydrogen, magnesium, chloride and sulphate ions ; group (2) waters are characterized by the presence of concentrations of calcium and bicarbonate ions at least as important quantitatively as the sodium, chloride and sulphate ions, and by the virtual disappearance of hydrogen as a major ion ; while group (3) waters are dominated by calcium and bicarbonate ions with sodium, chloride and sulphate assuming a relatively unimportant position. These general relationships may be seen in fig. 2 where the surface waters of the district have been assembled into groups according to their total ionic concentration. The mean percentage composition of each group is shown in the figure together with the number of localities included in each group. It will be seen that as the total concentration of ions increases the domination of sodium, chloride and sulphate ions is progressively supplanted by the increasing importance of calcium and bicarbonate ions. If it is assumed as a first approximation that chloride is not significantly supplied by solution from the drainage area (see later), then a consideration of the ratio of the percentage of chloride to the percentage of other ions will enable one to assess the extent of the contribution made by rock solution to the concentration of the other major ions. Where the ratio of the percentage of chloride to the percentage of the ion in question remains constant, there can be little contribution of that ion from solution of the rock, where however this ratio increases, the gain must clearly derive from terrestrial sources. On this basis it will be seen that much the most important terrestrial contribution consists of

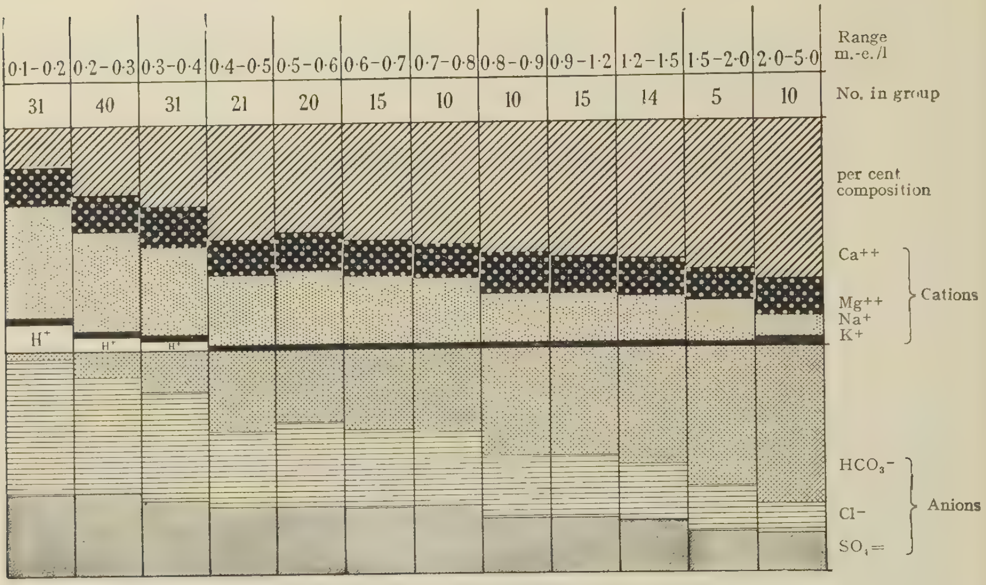

Fig. 2.—The relationships between composition and total ionic concentration in the surface waters of the Lake District. The percentage compositions shown are mean values calculated for each concentration group.

calcium and bicarbonate ions, while considerable quantities of magnesium, potassium and sulphate must also be so supplied, whereas the contribution of sodium must be small.

The observed distribution of the major ions can clearly be explained by postulating a common original composition for all the surface waters, closely approximating to that of the high tarns of the area, that is a dilute water dominated by sodium, hydrogen, chloride and sulphate, this ‘ primitive ’ composition being subsequently modified by contact with rock and soil to an extent determined by the geology. It has been shown by Gorham (1955) that the average composition of the rain falling on the Lake District does in fact closely resemble that required by such a postulation, the rain-borne electrolytes being derived from two main sources (1) material carried from the sea in solution in the rain or as fine salt particles formed by evaporation of sea-spray, and (2) materials liberated into the atmosphere by industrial activities, these consisting largely of sulphuric acid with minor proportions of hydrochloric acid, nitric acid, ammonia, calcium and potassium. The rain then consists of a much diluted sea-water acidified with sulphuric acid, having the same order of concentration of ions as that found in the most dilute Lake-land waters and dominated by sodium, magnesium, hydrogen, sulphate and chloride. This ‘ primitive ’ composition remains practically unaltered in many of the most dilute examples of the surface waters. The first modification which takes place is derived from the replacement of the hydrogen ion by calcium, magnesium and potassium ions by reaction with rock silicates and carbonates with the liberation of carbonic and silicic acids, the latter remaining in solution as dissolved ‘ silica ’. Further modification takes place on contact with more calcareous rocks by the appearance in solution of increasing proportions of calcium as the bicarbonate, this effect being of little importance where the drainage system lies in the Skiddaw slates and Borrowdale volcanics but becoming significant in the areas of Coniston limestone and

Bannisdale slates, and dominant where the influence of the Carboniferous rocks is felt.

It has been assumed that little or no chloride is derived from the drainage system, but that practically all comes from the sea. This assumption is based on the similarity between the chloride content of average rain and that of the dilute surface waters. The assumption is further supported by a consideration of the proportions of sodium and chloride found in the surface waters, in the rain, and in the sea. In fig. 3 the concentrations of sodium are plotted against chloride in milli-equivalents per litre. The solid line represents the proportions of sodium to chloride found in the sea and in the rain falling on the area (the proportions in the rain coinciding almost exactly with those in the sea). It will be seen that with few exceptions, the points representing the proportion of sodium and chloride in the surface waters lie close to those found in the sea, although some small gain in sodium is often apparent.

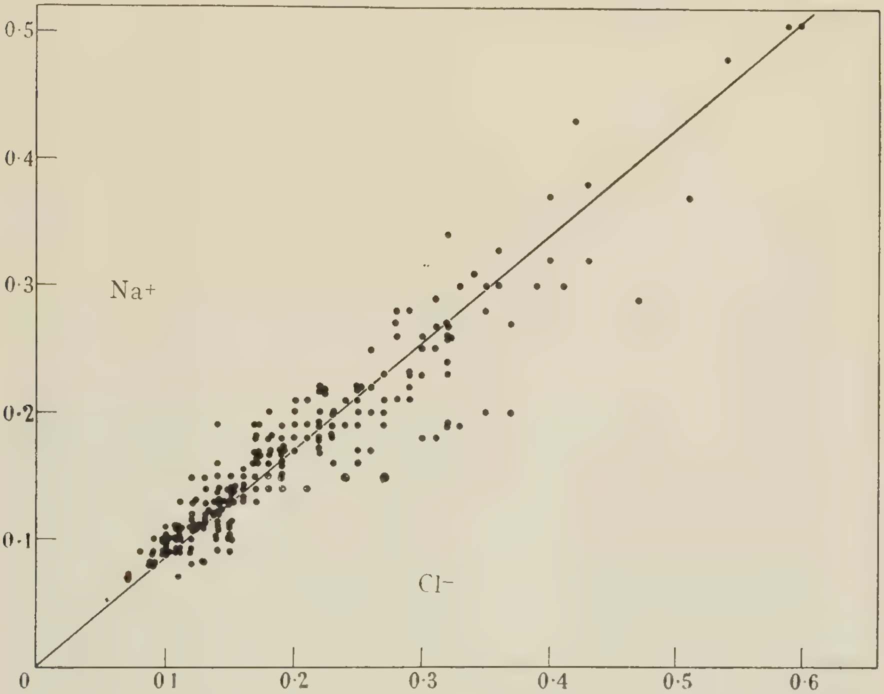

FIG 3.—The relationships between sodium and chloride concentration in the surface waters, compared with that in sea-water and rain water (solid line).

Although geology is the main factor in the production of differences in surface water composition, geographical position may also have some influence. In fig. 1 it will be seen that the total ionic concentration shows a tendency to increase towards the west, and analysis of these waters shows that they do not follow the general pattern of composition illustrated in fig. 2. In these waters the influence of the sea is more strongly felt than in more central areas and sodium and chloride continue to be the dominant ions at higher total ionic concentrations than elsewhere.

DISCUSSION.

The quantitative differences in composition of the Lake District waters have been shown to be due to variation in concentration and proportion of those materials which I have called major ions. It is unlikely however that any of these substances is a limiting factor from a biological point of view. It would seem then that these gross chemical differences cannot help to solve the problems of plant and animal distribution. Nevertheless there does seem to be a general correlation between increasing ionic concentration and increasing algal productivity (see Lund). If this is the case, then perhaps one should consider such factors as ionic concentration as being symptomatic of other and biologically important differences. Increasing concentration of ionic material in the surface waters reflects increasing solubility and decay of the rocks constituting the drainage system, which must mean that not only are the major components of the rocks made more rapidly available for plant growth, but also the many minor constituents which may well play a decisive role. One must add to this the cummulative effect of the formation of soils in those areas subjected to rapid solution and erosion, with the consequent presence of large masses of finely divided rock material which must lead to more rapid solution and utilization of those elements necessary for growth. It also becomes increasingly clear that algal productivity may not be solely dependent on the distribution of inorganic materials, but also on soil-derived organic substances which seem to be essential requirements for at least some algal species. Should this prove to be a general condition for efficient algal growth, differences in productivity might well be traced to the presence or absence of organic soils in the drainage basins as was suggested by Pearsall (1921 and 1924).

Other differences between water bodies may arise merely from differences in the volume of water contained in them. A large volume of water tends to be more stable in composition than a small one, thus the small mountain waters are subjected to continual fluctuations in composition depending on the direction of rain-bearing winds. Southerly winds usually bring rain containing sulphuric acid with consequent rapid lowering of pH and rise in sulphate concentration, while westerly winds bring sea-spray with dominating quantities of sodium and magnesium chlorides and rising pH. Larger masses of water, or those draining soluble rocks, are little affected by such fluctuations, the former because they are an integration of many compositional variations over a long period of time, and the latter, because such fluctuations are overwhelmed by the comparatively large and stable contribution of the rock. Such rapid environmental changes as occur in the small dilute tarns might well prove to be an important ecological factor.

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CHEMICAL ANALYSIS IN ECOLOGY ILLUSTRATED FROM LAKE DISTRICT TARNS AND LAKES. 2. ALGAL DIFFERENCES

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(With 3 text-figures and 1 table.)

In almost all bodies of water in Britain there is at least one period of the year, usually sometime between spring and autumn, when the physical conditions favour a more or less rapid increase in the numbers of algae. If, then, a regional survey of many bodies of water is made during this period, it may be expected that a majority will contain algal populations whose size reflects their characteristic productiveness. This will be so even if there is only one occasion of sampling, as was the case for about half of the one hundred and eight tarns whose standing crops of phytoplankton have been estimated. The rest of the tarns were sampled from two to five times with, in most cases, a gap of about a year between each occasion of sampling. All the tarn waters were analysed by Mr. J. Heron and Mr. F. J. Mackereth, and lie within the area surveyed by Mr. Mackereth in the preceding article. Standing crops are, of course, not necessarily an accurate measure of production. Nevertheless, it is generally the case that productive bodies of water have large standing crops while it is difficult to imagine an unproductive body of water possessing relatively large standing crops of plankton over prolonged periods of time.

It is, therefore, possible to make broad comparisons between the size of the standing crops of plankton and the concentrations of dissolved substances in these tarn waters. It is clear from fig. 1 that on the average, the higher the total content of ions the greater the crop. This, in turn, means that the more calcium bicarbonate there is, the greater is the frequency of larger standing crops, for the basic inorganic constitution of the tarn waters comes from rain water, and increases in the total ionic content arise from solution of the rocks and soils. In nearly all cases this solution is dominated by calcium bicarbonate. Very rarely calcium sulphate is also important but although there are differences in the amount of potassium this element never forms more than a small fraction of the total ions present. There is no evidence that anything except a very large growth of plankton causes any marked reduction in the calcium content of water and even when this does happen it is not from incorporation into the algal cells but from extracellular precipitation as carbonate related to the amount of photosynthesis by day. The relationship with calcium is, therefore, indirect but there might be a direct relationship with bicarbonate. However, the latter is only likely if the crop is very large, probably of the order of ten thousand cells per ml. Moreover, in soft waters a marked rise in pH would be observed if such a situation arose. There are many analyses for the lakes in this area (see later), in some cases for almost every week for ten consecutive years. All are softwater lakes and even in the most productive of them no appreciable rise in pH has ever been recorded. Further, it is invariably the case in the most productive of them (e.g. Esthwaite Water, Windermere, south basin and Blelham Tarn) that the amount of bicarbonate increases in summer just when there are commonly large crops of algae and this happens every year irrespective of the algal production. Indeed, it seems that the increase in bicarbonate is related to reduced rainfall and increased evaporation for it tends to be most marked in the warmer and drier summers. Lastly, if the plankton diatom *Asterionella formosa* Hass is taken as an example, an analysis of its cells shows that the carbon content is so small that the largest crops seen in these lakes over a period of twenty years could be produced from the available supply of bicarbonate without allowing for the carbon dioxide present in the water or its replenishment from the atmosphere (fig. 3, top left). There is, then, certainly no suggestion of any shortage of bicarbonate, and we must look for some other substances controlling the productivity of these tarns.

The other major ions, magnesium, sodium, chloride and sulphate are all present in such large amounts in the water relative to those found in algal cells (cf. *Asterionella*, fig. 3 top left), that there can scarcely be any doubt that they are present in excess of what is needed. Only potassium of these major ions is present in rather small amounts. Again, in the tarns surveyed, with increasing amounts in the water there are, on the average, more algae present. However, algal cells contain little potassium (e.g. Scott, 1943, 1944, 1945 a & b; Burlew, 1953; Whipple & Jackson, 1899. Unpublished analyses of planktonic and other freshwater algae by Mr. J. F. Mackereth show similar amounts). Moreover, if it did limit algal production the relationship should differ from that seen in fig. 1; that is, tarns with very large crops of algae as well as those with very small ones should show low potassium concentrations in the water. Yet there are four tarns with crops far larger than the other, averaging about one million cells per ml. so that the water was green and these are the ones with the highest potassium concentrations in the water.* Again the relationship appears to be indirect.

Only nitrate of the minor ions was estimated in the tarns and then in only fifty-four of them (fig. 1). The differences in the standing crops are not very marked but the lower concentrations of nitrate are on the whole correlated with the larger crops. Even if this suggests an appreciable utilisation of nitrate we have no means of knowing whether the lower concentrations are such as to limit production. There is, however, another set of data available for consideration of both major and minor ions, namely observations on the lakes in the area (figs. 2 & 3). The figures for bicarbonate carbon, nitrate nitrogen, phosphate phosphorus, silicate silicon and standing crops of phytoplankton are based on samples taken at regular intervals for at least two years (ten years in the case of Windermere south basin and Esthwaite Water) and at irregular ones over six to nine years. The figures for the other ions are only based on a few analyses but since, in such bodies of water as these, the retention times are relatively long and the ions concerned are, with the possible exception of potassium (see earlier), not appreciably removed by incorporation into organisms, their concentrations are unlikely to vary markedly. They represent the mean values for the concentrations in the rain falling on the catchment area over a considerable period of time and it is unlikely that they will ever be more or less than twice or half the values here recorded.

The lakes with the larger amounts of carbon, nitrogen and phosphorus (but not silicon) are those with the larger crops and the increases in these nutrients and crops in general follow one another (fig. 3). However, while the ratio of nutrients is of the order of two to five times between the highest and lowest (fig. 2) those for crops reach to over a thousand times between highest and lowest (fig. 3). Nor are these maximal figures very peculiar, a comparison of the average standing crop between Wastwater and Esthwaite Water, for instance, shows much the same relationship. It is, therefore, difficult to explain the differences between the productive and unproductive lakes on the basis of increasing supplies of carbon, nitrogen and phosphorus or any of the major ions. Comparison between the amounts of these elements in the water and in the cells of the common plankton diatom *Asterionella formosa* leads to the same conclusion apart from silicon. Yet even here comparison of the silicon contents of the lake waters (fig. 2) shows that something

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* The fifth tarn in this group rich in potassium had a small crop of plankton. It has, however, turbid water from fine clay particles so that light is the limiting factor.

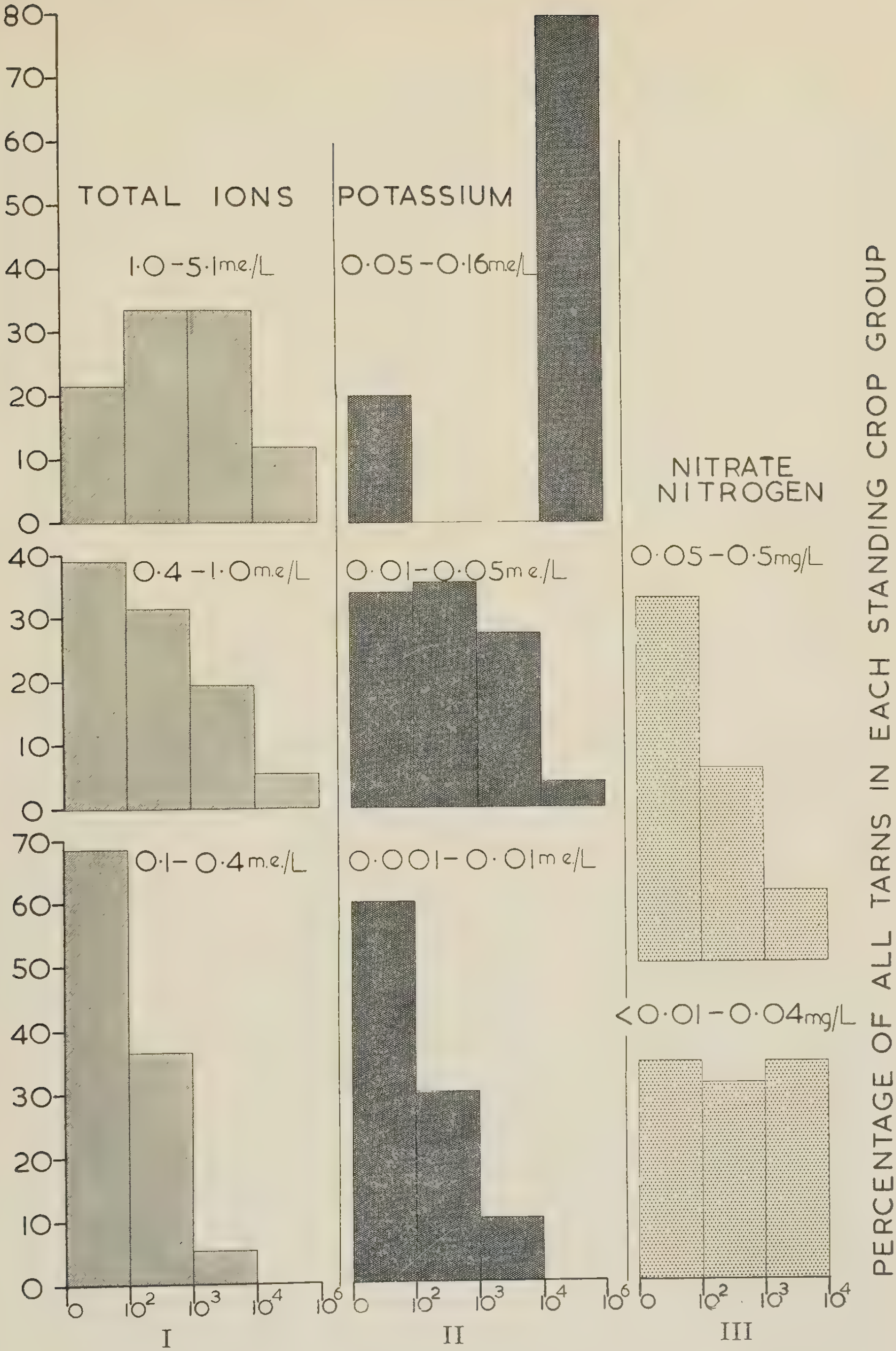

FIG. 1.—Standing crops of phytoplankton in one hundred and eight tarns in the English Lake District in relation to the content of total ions, potassium and nitrate nitrogen in solution. I. Total ions. The tarns have been divided into three groups, each one containing approximately the same number of tarns but differing in their content of the major inorganic ions (Ca, Mg, Na, Cl, K, SO_4 and HCO_3) expressed in milli-equivalents (*m.e.*) per litre. These ions represent more than 99% of the total ions in solution. In each of these three groups the number of tarns with standing crops within the limits (expressed in cells per ml.) shown on the horizontal axes has been expressed as a percentage of the whole (vertical axes). II. Potassium. The tarns have been divided in the same way as for total ions except that while the two groups containing the smaller amounts of potassium in solution consist of approximately equal numbers of tarns, the group with the largest amount (0·05 -0·16 *m.e.* per L) consists of only five tarns and is treated separately for the reason given in the text. III. Nitrate nitrogen. Only fifty-four of the tarns are here represented, being divided into two groups containing approximately equal numbers of tarns. Since the amount of nitrate nitrogen is but a very small fraction of the total ions in solution the analytical results are expressed in mg/L ; otherwise the data are treated in the same way as for total ions.

else must be responsible for the richness of the productive lakes in this and other plankton diatoms even though, once that something is available, production is often limited by the amount of silicon present (Pearsall, 1932; Lund, 1950, 1955; Canter & Lund, 1951).

It is also possible to follow the rise and fall of a plankton population with the changes, if any, in the concentration of any of the substances mentioned. However, except for phosphate, silicate and nitrate it is scarcely ever possible to see any apparent relationships. The phosphate concentration may show a fall as algal numbers rise (e.g. Gardiner, 1941) but it has been shown that the correlation between minimal phosphate concentration and the maximal population does not necessarily mean that phosphorus is acting as a limiting factor (Lund, 1950; Mackereth, 1953). Very large populations of diatoms at least may develop in the absence of an equally marked change in the phosphate concentration. The nitrate concentration may show a fall as a crop of plankton increases (e.g. Lund, 1950, figs. 1–4, 6) but the relationship is often rather irregular and the fall in nitrate may continue as the crop concerned declines and before a large crop of other algae has arisen to take its place. Indeed in the productive lakes of the English Lake District the change in the nitrate concentration is almost exactly the reverse of that of the bicarbonate concentration, previously mentioned. In a lake such as Esthwaite Water it always falls to low values in summer and, in general, the drier and warmer

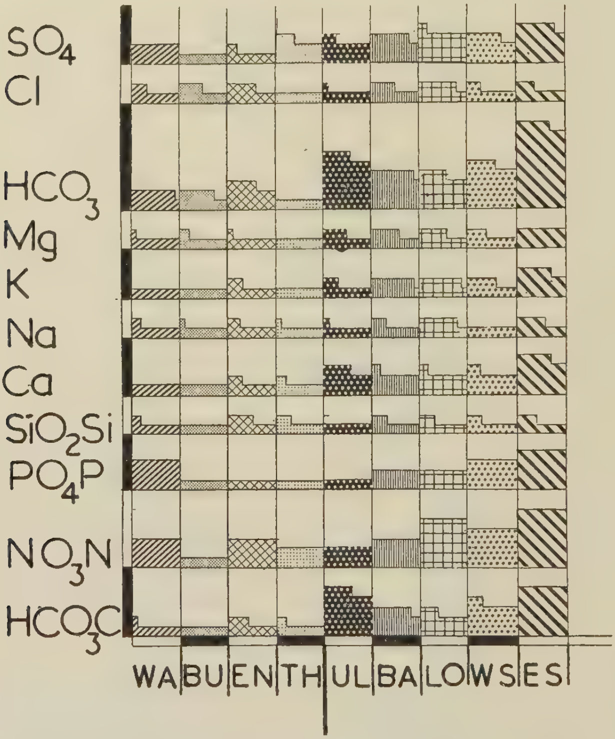

Fig. 2.—Maximum recorded concentrations of certain ions in 9 lakes in the English Lake District expressed as ratios. In each case the concentrations are expressed by the enclosed areas, the lake with the least amount of the ion concerned being represented by the smallest area and the others by areas proportional to this basic areal unit. For the names of the lakes see fig. 3.

this period is, the lower the concentration falls. While a direct relationship between this summer minimum in nitrate concentration and the growth of algae cannot be ruled out, the data at present available suggest that this is not the case, for low concentrations of nitrate are more clearly correlated with climatic conditions. For silicate alone there seems to be good evidence that it acts as a limiting factor but this only applies to certain plankton algae which need a fixed amount per unit area of cell wall and cannot increase markedly in numbers when the concentration falls below approximately 0·5 mg SiO_2 per litre (Einsele & Grim, 1938; Pearsall, 1932; Lund, 1950, 1955).

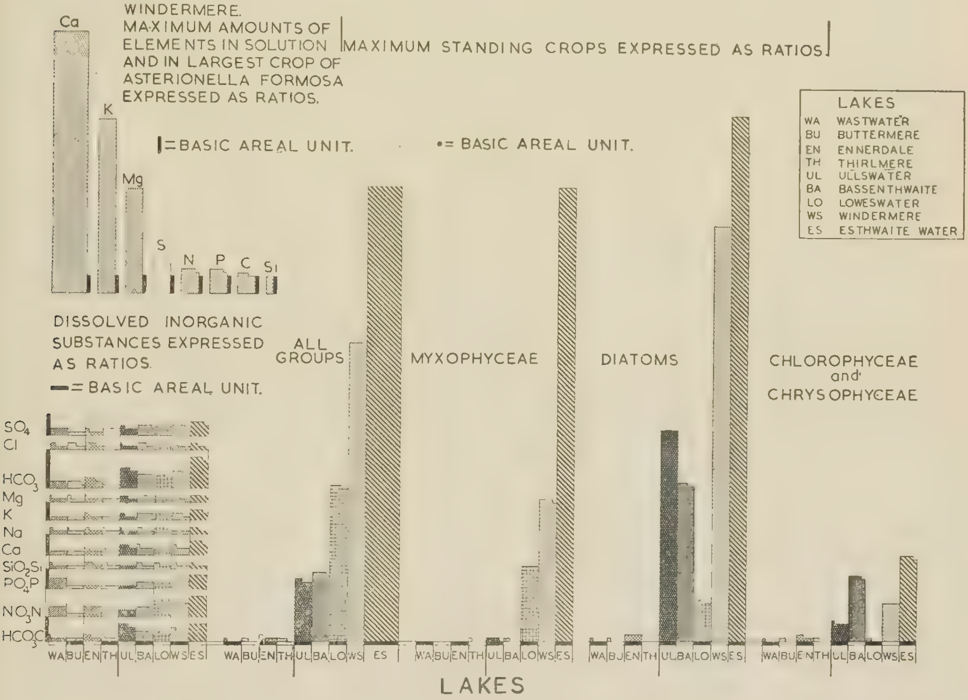

FIG. 3.—Maximum recorded concentrations of certain ions in lakes in the English Lake District and maximum recorded standing crops of phytoplankton all expressed as ratios. Also amounts of certain elements incorporated in the largest recorded standing crop of *Asterionella formosa* Hass. in Windermere compared with the maximum recorded amounts of these elements in solution; in this case the amount in the cells of *Asterionella* is the basic unit of area. The chemical data for the lakes is the same as in fig. 2 and the ratios between the algal crops are expressed in the same manner.

It may be that the substances for which analyses are commonly made very rarely determine the abundance of algae so that others should be estimated, if suitable analytical techniques for routine observations exist. Experimental work with algae grown in artificial solutions shows that some algae need iron, manganese, boron, molybdenum, vanadium, cobalt and copper. Iron is presumably needed by all and some or all of the other elements may well be necessary for the growth of many or all algae. Spectrographic analyses show that further elements are present in algal cells in amounts similar to or greater than these trace elements (Table I). It is to be expected that traces of most of the elements present in a lake should be present in or on* the cells of plankton algae but in the table it is noteworthy that elements such as nickel, lead, zinc, titanium are present in far greater amounts than cobalt, molybdenum and vanadium. It does not, of course, follow that these substances play any vital part in their metabolism but there does not seem to be any proof that they do not do so. Recently it has become clear that many algae need accessory organic growth factors such as vitamins (e.g. Provasoli & Pintner, 1953). Another complexity is that iron, for example, can scarcely be obtained from its simple inorganic salts but may be obtained from organic iron complexes (chelating substances) or even from colloidal or solid particles (Goldberg, 1952). Lastly, the concentration of a substance in the water at any one moment is not necessarily a true indication of the amount available, since this may be merely the momentary state of a more or less rapidly self-adjusting equilibrium. Examples are the carbon dioxide–carbonic acid–bicarbonate carbonate system and probably phosphate which is present as free and absorbed ions.

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* It is scarcely possible to determine whether or not minute traces of substances are on or in the cells particularly since they are so commonly covered by a thin (*Asterionella*) or thick (many *Staurastrum* spp.) layer of mucilage.

TABLE I.—Spectrographic analyses of lake water and algae. Windermere Water, *Asterionella formosa* Hass. and *Staurastrum paradoxum* Agg. collected from Windermere in November 1950, January 1951 and August 1951 respectively. *Prasiola crispa* (Light) Menegh. from below Puffin burrows on the Farne Islands, Northumberland in July 1948. All the samples dried to a constant weight at 105°C after being washed in distilled water. Analyses of Windermere Water and *Asterionella* by Dr. R. L. Mitchell of the Macaulay Institute of Soil Research and of the other algae by members of the chemistry staff of the Atomic Energy Establishment, Sellafield, Cumberland.

Element	Windermere water μg per Kg	μg per gm dry weight		
		Asterionella formosa	*Staurastrum paradoxum*	*Prasiola crispa*
Ag	>0·2	>0·5	>6·0	>2·0
Co	>0·1	>0·5	>6·0	>2·0
Cr	>0·3	>20	>10	>2·0
Mo	>0·1	>5	>6·0	>2·0
Ni	0·23	83	30	>2·0
Pb	>2·0	680	10	4
Ti	>0·5	1100	60	>20
V	>0·1	>5	>6	>2·0
Zn	>8·0	1240	>15	>40

It may, indeed, seem that water chemistry as it is practised is of little assistance in elucidating the causes of the abundance and periodicity of algae, partly perhaps because it is impossible to carry out as a routine all the analyses which may be necessary. We cannot, however, expect to obtain more than a partial understanding of these matters by such methods and there is a number of good reasons for continuing to carry out the standard water analyses. Observations on the natural habitat can show which algae are growing over any variation in the nutrient supplies. From the cultural approach alone it often appears that an alga cannot grow in the type of water in which it actually does so in abundance. This may be because of the difficulty of making culture solutions which are the same as or closely similar to the natural medium. However, cultural work in the laboratory is essential, for by this method alone can the environment be controlled. The observational and experimental approaches supplement and provide a check upon each other. There is as yet insufficient knowledge of the nutrition of these plankton algae to permit many definite statements. Indeed, it will not be surprising to find that the views put forward here about the relationship between the major ions dissolved in water and algal production are not wholly correct. The standard analyses have led to some advance in our knowledge of the ecology of algae. The limitation of growth of some diatoms by silica was first suspected nearly sixty years ago (Whipple & Jackson, 1899)—a suspicion substantiated by later observations and chemical analyses of the cells and media in which they grew. Moreover, despite what has been said earlier, the concentrations of phosphates and nitrates do fall to very low levels at times in some bodies of water and may well be among the commoner substances limiting algal production (see also Lund, 1954, pp. 498-501). In order to understand the chemical basis of algal periodicity and abundance in nature we must consider each species separately. The usual observational methods only give a broad generalized picture together with hints on how to proceed further. The biochemistry of one alga is unlikely to be exactly the same as another though a number may possess some features in common. Having discovered a requirement for one species it is relatively easy to apply similar tests to others. It is, of course, ridiculous to consider chemical relationships *in vacuo* as it were. The physical and biological relationships of the algae must be considered. Indeed, taxonomy is the basis of chemistry in this context. The ecology of algae should be attacked on a broad front with a keen eye for the main chance. Ideally, prolonged observations on natural populations would be combined with laboratory experiments and analyses of cells. Time and the facilities available never permit this ideal to be realised fully so that deciding how much to attempt and in what manner is of great importance.

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CHEMICAL ANALYSIS IN ECOLOGY ILLUSTRATED FROM LAKE DISTRICT TARNS AND LAKES. 3. FAUNISTIC DIFFERENCES

By T. T. MACAN.

(With 1 table.)

The study of the faunistic differences and their possible correlation with chemical data in various bodies of water falls into three stages. In the first the systematics of the various fauna are tackled, and groups in which the identification of the various species is unambiguous are selected for the next stage. In this stage are sought factors common to the different localities in which each particular species is found. Finally the nature of any such observed correlations may be studied experimentally. This essay lies within the second stage and deals with two groups of animals, the Corixidae (Hemiptera) and the freshwater snails. In such a study it is common practice to analyse the water for various inorganic substances, which it is easy to do and which gives exact results. The intention here is to discuss the value of doing it.

There is a succession of species of corixid as organic matter accumulates on the bottom of a pond or lake, and the species which are present at any given stage of accumulation depend on whether conditions are trending in a direction that will lead to bog or to fern (Macan, 1954). Further in one body of water conditions vary from place to place according to the degree of exposure to wave action or the nearness of a stream bringing in silt, and the corixid population varies with them. These animals, therefore, are not likely to show a close relation with the *general* conditions as revealed by an analysis of a sample of water taken from the middle or from the outflow. However it is possible to use species of snails to arrange, into groups, the tarns which have been studied. This has been done in the Table (p. 174).

Group I at the bottom of the table has no snails and the waters of all the tarns in it are in Lund's ' low ' class.* That there is a correlation seems likely. All the remaining tarns are in Lund's ' mid ' or ' high ' classes. There is a tendency for the ionic concentrations to be bigger as the top of the table is approached, and four of the five tarns in the ' high ' class are in the top group, but this is no more than a tendency and there is a big range in each group. At the outset then close correlation between any species and any particular proportion or total concentration of the six ions which Mackereth has studied is not to be expected.

In Group II *Limnaea pereger* is the only snail. Why are there no other species, and in particular why, since it is a widespread species not apparently requiring special conditions as the others may, is *Planorbis albus* absent? There is nothing in the chemical analysis to account for it. It is noticeable, however, that those tarns in this group which have a relatively high ionic and calcium content are small or extensively overgrown with vegetation, and these may be conditions that are unfavourable for *P. albus*.

The next group (III) with both *L. pereger* and *P. albus*, may be taken as the standard against which the others are compared. In Group IV there are 4 tarns, all with the two species mentioned, all with *L. palustris* as well, and all with one or more of three other species none of which is found in any other tarn. On the snail fauna the group appears to be homogeneous, but, when the chemical analyses are examined, nothing peculiar to the four tarns is evident. What does set them apart from the rest is their size or their retention of flood water. Two of the tarns are bigger than any other, having approximate areas of 171,100 and 52,700 square yards, and one of these runs into a third and may well supply it with snails as well as with water. The fourth tarn is quite small but is unlike the rest in that after rain there is a great increase in volume and a slow return to normal level. It seems likely that these tarns, being less affected by rainfall, are more stable chemically and for that reason harbour their peculiar assemblage of snails, which, it may be noted, is characteristic of lakes. Lakes differ from tarns mainly in being much bigger.

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* See Lund's fig. 1, column headed total ' ions.'

The outstanding feature of Group V is the scarcity of *L. pereger*, the species that occurs in every tarn in every other group. It occurs in but one of the four tarns and is very scarce there. Again there is no particular combination of ionic concentrations common to all the tarns. The feature that does characterize them is their location in woodlands, and it may be surmised that the great mass of dead leaves that they receive each year produces conditions unfavourable to *L. pereger*, though it must be borne in mind that they are also more shaded than other tarns. Another surmise is that, if organic substances could be identified and measured as easily as inorganic compounds, some chemical peculiarity of the tarns in this group might be found.

Each of the eight tarns in Group VI contains *L. pereger*, generally *P. albus*, and one or more of four other species. Some of them have a higher ionic concentration and particularly more calcium than other tarns, and it is probable that the occurrence of *L. stagnalis* is related to this. Others, however, are less rich in ions than tarns in other groups. One feature common to all these tarns is that they lie to the east of Windermere near the boundary of the soft rocks. It is not impossible that the populations of some of the species are maintained by immigration from the nearby calcareous rocks; *Planorbis complanatus* tends to appear and disappear.

Of the Corixidae, *C. scotti* occurs in all the groups and *C. castanea* has an equally wide range though occurring less often because many tarns lack the thick vegetation to which it appears to be more or less confined. *C. distincta* and *C. fossarum* have a narrower range, and *C. praeusta*, *C. bonsdorffi* and to a less extent *C. linnei* are found mainly in Groups V and VI. The last three species are associated with organic matter from an outside source such as dead leaves or animal fouling. Groups of tarns based on the corixids do not correspond exactly with groups based on snails, and, like them, do not show any chemical peculiarities.

In the lakes that Lund has called unproductive only *L. pereger* is present. *Planorbis albus*, *P. contortus*, and *Physa fontinalis*, and *Valvata piscinalis* occur in nearly every one of the others; *Limnaea palustris* occurs in over half; and six other species have been found occasionally (Macan, 1950, table II). A comparison of corixid faunas is best based on the species found in exposed places, since conditions within a big reed-bed may be unrelated to the general conditions in the lake. If this be done, the lakes fall into three groups, the least productive with *C. dorsalis* (*striata*) and *C. scotti*, the most productive with *C. dorsalis* and *C. falleni* and an intermediate group with *C. dorsalis* only (Macan, 1955). Lund has already drawn attention to the slight chemical differences between the lakes.

In conclusion: this study of two groups of animals and Mackereth's analyses of six ions and total ionic concentration have confirmed a relationship between certain snails and calcium concentration, a relationship that has been known for many years (see, e.g. Boycott, 1936) but otherwise has not brought to light anything more than vague general correlations. Something more positive might have been more gratifying to the investigators, but the important thing is perhaps that it is now possible to make a statement that was not possible before. The writer is keenly aware of the advantages of working under circumstances where collaboration of this kind is possible.

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TABLE.—Thirty-seven Lake District Tarns showing: the common species of Corixidae according to a somewhat subjective impression; the species of snail found during a search lasting an hour; and the concentration of certain substances in parts per million unless otherwise stated. (The situation of these tarns is shown by Macan (1950, fig. 1))

Group	Tarn	Corixa praeusta	Cymatia bonsdorffi	Corixa linnei	C. fossarum	C. distincta	C. scotti	C. castanea	Limnaea stagnalis	Planorbis crista	P. complanatus	Limnaea palustris	Valvata piscinalis	Physa fontinalis	Planorbis contortus	P. albus	Limnaea peregor	Total ions milli equiv./litre	Ca	Mg	Na	K	Cl	SO_4	NO_3
VI	Rather Heath 6	X	X				X				X	X				X	X	1·5	20·0	2·6	4·7	0·9	9·8	12·2	0·4
	Rather Heath 1		X		X		X		X	X	X	X				X	X	1·4	19·8	2·1	5·1	0·7	9·1	12·2	0·4
	Lindeth	X	X	X			X				X	X				X	X	—	5·5	—	—	—	—	—	—
	Podnet	X	X				X				X					X	X	0·6	6·2	1·0	5·0	0·5	9·4	11·1	0·03
	New	X	X			X	X			X		X				X	X	0·8	6·0	1·7	6·2	0·7	12·5	11·4	0·03
	Cleabarrow	X		X		X	X	X			X	X				X	X	1·25	14·0	2·4	6·2	1·4	10·0	17·8	—
	Little Ludderburn		X				X	X				X				X	X	1·4	16·3	3·5	5·1	0·6	8·2	13·2	0·2
	Batemanfold							X				X					X	0·8	8·5	1·5	5·0	0·4	8·2	12·9	0·03
V	Lost			X	X		X	X				X				X		0·9	10·5	1·4	5·0	0·8	9·1	10·3	0·1
	Cacer				X	X						X				X		0·7	8·8	0·9	4·2	0·4	8·8	8·9	—
	Rose Castle	X		X		X	X									X		0·9	9·8	2·1	4·3	0·4	11·4	10·2	—
	Slew	X	X	X		X										X	X	0·6	6·5	0·6	3·5	0·5	8·0	9·6	0·3
IV	Wise Een				X	X	X	X				X			X	X	X	0·5	4·9	0·9	4·2	0·5	7·5	9·7	—
	Wray Mires				X	X	X	X				X	X		X	X	X	0·5	5·0	0·8	4·4	0·5	8·8	9·5	0·01
	Tarn Hows						X			X		X	X	X	X	X	X	0·6	5·3	1·3	4·0	0·2	8·9	5·3	—
	Wharton						X					X	X	X		X	X	0·7	7·4	1·3	3·8	0·5	7·3	8·7	0·01

III	Blelham F.P.			X					X	X	0·8	9·6	1·5	4·1	0·6	12·3	9·8	0·5
	Clay Pond			X	X				X	X	1·1	11·7	2·4	7·8	0·8	11·4	15·0	—
	Gill Head R.	X				X			X	X	0·7	5·9	1·6	5·5	0·6	11·4	12·0	—
	Arnside					X			X	X	0·6	5·3	1·1	4·5	0·6	8·1	7·8	0·08
	Knipe					X			X	X	0·9	9·7	1·9	5·3	0·3	10·6	9·6	—
II	Black Beck Moss		X				X			X	0·7	7·7	1·3	5·1	0·5	9·2	10·7	0·2
	Wray Mires F.P. 2		X		X	X	X			X	0·6	4·7	1·3	6·2	0·6	12·5	10·3	0·03
	Robinson		X			X	X			X	0·6	6·2	1·1	4·7	0·5	8·7	10·8	0·02
	Moss Eccles			X	X	X				X	0·5	5·2	1·0	4·2	0·4	6·8	9·1	—
	Three Dubs				X	X				X	0·5	3·9	0·9	4·3	0·1	6·1	10·2	—
	Green Hows R.					X				X	0·7	6·6	1·2	6·0	0·6	11·2	13·6	0·07
	Brigstone 2					X				X	0·5	5·1	0·6	3·3	0·3	6·1	6·1	0·1
	Gill Head F.P.					X				X	0·6	4·1	1·1	5·5	0·8	10·5	10·7	0·03
	Hodson					X	X			X	0·5	4·9	1·1	3·7	0·2	4·9	9·6	—
	Nor Moss					X	X			X	0·6	6·4	0·8	4·2	0·5	8·2	13·2	0·1
	Wray Mires F.P. 1					X	X			X	0·6	4·0	1·3	5·8	0·7	11·4	10·1	0·03
	Wray Mires F.P. 3					X	X			X	0·7	4·7	1·3	6·2	0·6	12·9	10·1	0·03
I	Brigstone 1					X					0·4	2·8	0·5	3·2	0·5	5·8	7·1	0·1
	Blea										0·3	1·3	0·5	2·6	0·4	3·9	4·2	—
	Lingmoor					X					0·3	2·2	0·7	3·3	0·3	5·9	6·4	—
	Harrop										0·2	1·5	0·4	2·1	0·1	3·4	4·8	—

ON THE HYBRIDIZATION OF THE COMMON SPOTTED ORCHID, DACTYLORCHIS FUCHSII (DRUCE) VERMLN., WITH THE MARSH ORCHIDS, D. PRAETERMISSA (DRUCE) VERMLN. AND D. PURPURELLA (T. AND T. A. STEPH.) VERMLN.

By J. Heslop-Harrison.

(With 6 text figures.)

Hybrids arising from the crossing of the common spotted orchid, *Dactylorchis fuchsii* *, with the marsh orchids have long been a source of interest to field botanists—and justly so, considering the remarkable appearance of mixed colonies when plants seemingly of hybrid origin outnumber the parents. Such colonies manifest a multiformity which would seem to suggest that they contain not only parents and first generation hybrids, but also later hybrid generations and back-crosses. And yet *D. fuchsii* is a diploid species, with a chromosome number of $2n=40$, and the marsh orchids with which it commonly hybridizes in the British Isles, *D. praetermissa* in the south of England and the Midlands, and *D. purpurella* in the north of England, Scotland and Ireland, are tetraploids, with $2n=80$. The F_1 in each instance may be expected to be triploid and of low fertility, a circumstance which would seem to preclude the appearance of later hybrid generations and back-crosses. In this paper I propose to apply some simple methods of morphological and cytological investigation to elucidate the structure of some of these familiar hybrid colonies, and in particular to see how far we are justified in looking upon them as ' hybrid swarms ' in the sense, e.g., of Turrill (1948), in which " . . . in addition to first crosses, there are all sorts of back-crosses with the original parents and between segregates ".

The multiformity of a hybrid population can, of course, be no more than a subjective impression until some reasonably precise form of analysis is applied. Depending upon the mode of inheritance of the various characteristics differentiating the parents, hybrid individuals in mixed populations will be recognizable phenotypically by their intermediacy between the parental species. In analysing the composition of such populations, what is required is a means whereby the complex of characteristics of each plant is assessed in relation to parental norms. This is, of course, an unattainable ideal, but an approach to it can be made by assessing in each plant a small selection of characters giving the required form of discrimination. This is the ' hybrid index ' method of Anderson, used first in the study of natural hybridization in North American species of *Tradescantia* (Anderson, 1936). As pointed out by Stebbins (1950), it is essentially a version of the statistical principle of discriminant functions, and the general concept dates from the anthropometrical investigations of Karl Pearson. The index is compounded for each plant by adding together scores awarded according to the expression in it of each of a selected group of the features which differentiate the presumed parents. To make the index more sensitive to variation in characters thought to be of greater discriminatory value, it is possible to weight the scores awarded to them differentially. Carried out with attention to the parental variances, this is in fact the basis of the statistical discriminant function : applied arbitrarily, it is open to the criticism that the final distribution obtained may be little more than an expression of the opinion of the investigator formed on his first approach to the population.

The Anderson hybrid index technique can be applied in investigating the structure of dactylorchid hybrid populations, but only with careful selection

* The taxonomy and nomenclature is that of Heslop-Harrison, 1954.

of characteristics for incorporation. As a general principle, ' intermediacy ' is most likely to be found in interspecific hybrids in those characteristics which are governed genetically by several genes, and it is naturally these characteristics, giving the clearest indication of hybrid origin, which are most satisfactory for incorporation in the index. It does not follow that these features are necessarily the most efficient for the discrimination of the parents. Again, in various metrical and meristic characters the variation of which is no doubt governed polygenically in parental populations, the phenomenon of hybrid vigour is likely to be encountered. This is indeed one of the most striking attributes of many dactylorchid hybrids, in which heterosis may be evident in stature, stem thickness and leaf and inflorescence size.

Taking first *D. praetermissa* and *D. fuchsii*, the principal differentiae may be listed as follows :

D. fuchsii ($2n=40$)	*D. praetermissa* ($2n=80$)
Stem solid	Stem hollow
Foliage leaves 3–6 ; bract-like upper leaves, 2–4.	Foliage leaves 3–4 ; bract-like, 2–3.
Lowest leaf obovate, rounded at the apex.	Lowest leaf broadest at the middle, acute.
Intense anthocyanin leaf-marking present in 50–100 per cent of individuals in most colonies.	Leaf marking absent except in individuals corresponding with var. *junialis* (*Orchis pardalina* Pugsl.)
Labellum markedly 3-lobed ; lobes subequal. Maximum width 8–12 mm.; colour rose-pink to white, patterned with regular divergent loops, pink, purple or lilac.	Labellum elliptical, obscurely 3-lobed, with rounded lateral and short, blunt central lobes. Maximum width 9–14 mm.; colour lilac-pink to magenta, obscurely patterned with centrally disposed dots and bars.
Spur narrow, cylindrical ; 1–2 mm. in width, 6–10 mm. in length.	Spur broad, cylindrical ; 7–11 mm. in length, 2·5–3·5 mm. in diameter.

A simple hybrid index may be compounded using six of these features. Five, in which a condition of ' intermediacy ' can be recognized fairly easily, are scored in three grades, ' 0 ' implying the modal condition in uncontaminated populations referable to *D. praetermissa*, ' 2 ' that in *D. fuchsii*, and ' 1 ', intermediate. The character of stem hollowness, important enough in distinguishing the *Majales* from the predominantly solid-stemmed *Eumaculatae*, is subject to considerable developmental variation. It is therefore convenient simply to score the presence of any cavity at all, the condition in *D. praetermissa*, as ' 0 ', and the absence of a cavity, as in *D. fuchsii*, ' 1 '. The index is then composed as follows :

Hybrid Index A.

Leaf number :	≤6	7	≥8
Score :	0	1	2
Leaf marking :	Absent	Light	Medium or heavy
Score :	0	1	2
Stem :	Hollow	Solid	
Score :	0	1	
Labellum, central lobe length :	≤1·5 mm.	1·6–1·9 mm.	≥2·0 mm.
Score :	0	1	2
Labellum pattern :	*praetermissa*-like	Intermediate	*fuchsii*-like
Score :	0	1	2
Spur width :	>2·8 mm.	1·9–2·7	<1·8 mm.
Score :	0	1	2

The southern English form of *D. fuchsii*, within the area where hybridization with *D. praetermissa* is frequent, corresponds with subsp. *fuchsii* (Heslop-Harrison, 1954). Using the hybrid index, the distribution obtained by scoring a sample of fifty plants from a typical woodland glade population in Butter Wood, near Greywell, Hampshire (fig. 1 a) shows a considerable spread, to be expected from the inherently high variability of the species in most morphological features. Some statistics for metrical and meristic characteristics in this sample are given in Table I. A sample from a population near Winchester, growing in a lightly grazed open grassland community dominated by the taller grasses including *Bromus erectus*, *Arrhenatherum elatius*, and *Brachypodium sylvaticum*, shows a similar mean stature (Table I, sample b) and reasonable agreement in leaf size. The distribution of the hybrid index of this population is not greatly different (fig. 1 b). A sample of the species taken from a population ocurring in ' short ' chalk grassland exposed to a considerable amount of grazing and dominated by the finer down grasses, *Festuca ovina*, *F. rubra*, *Briza media*, etc., on Telegraph Hill, also near Winchester, is only a little more than half the average height (Table I, sample c), and differs significantly also in leaf size. Nevertheless, the distribution of the hybrid index in a sample from this population is in reasonable agreement (fig. 1 c).

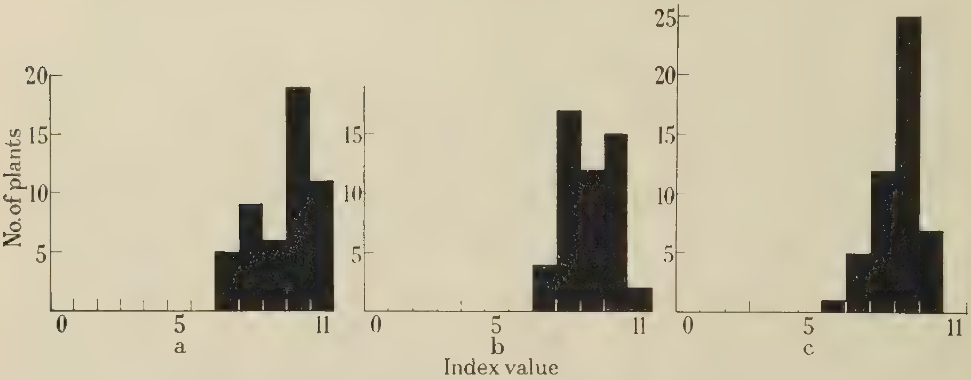

FIG. 1.—Distribution of Hybrid Index A in some populations of *Dactylorchis fuchsii*, a, 50 plants from a woodland glade population, Butter Wood, near Greywell, Hampshire. b, 50 plants from ' tall ' chalk grassland, near Winchester, Hampshire; c, 50 plants from ' short ' chalk glassland, near Winchester, Hampshire.

TABLE I.—Vegetative characteristics of some populations of *Dactylorchis fuchsii*.

Sample	Stature (cm)	No. of leaves	Length of largest leaf (cm)	Width of largest leaf (cm)
(*a*) Butter Wood, Hampshire (*n*=100)	42·1±0·98	9·2±0·15	12·6±0·37	2·60±0·08
(*b*) " Tall " chalk grassland, Hampshire (*n*=50)	40·2±1·07	8·1±0·18	13·6±0·36	2·28±0·08
(*c*) " Short " chalk grassland, Hampshire (*n*=50)	23·5±0·67	7·5±0·21	9·4±0·24	1·71±0·05

Evidently, then, the index as compounded above is not greatly sensitive to inter-population variation in *D. fuchsii* within the area in which hybridization with *D. praetermissa* is likely to take place.

Druce's original description of *D. praetermissa* (Druce, 1913) was based upon plants lacking any form of leaf marking ; essentially it applies to the tall form of fens, marshes and water meadows, the common marsh orchid of southern and eastern England. The distribution obtained by scoring the hybrid index, as compounded above, in a sample of fifty plants from a colony composed principally of plants agreeing with Druce's type description near Greywell, Hampshire is as in fig. 2 a. *D. praetermissa* shows an appreciable amount of inter-population variation, and since some of it affects just those morphological features in which the ' typical ' form is most clearly differentiated from *D. fuchsii*, the distribution of the hybrid index is influenced in aberrant populations. The problem of the ' internal ' variation in *D. praetermissa* will shortly be treated elsewhere, but one aspect is considered further below.

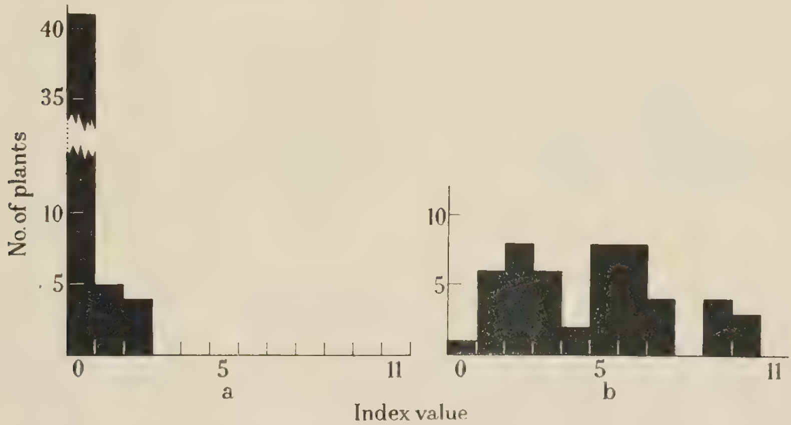

FIG. 2.—a, Distribution of Hybrid Index A in a sample of 50 plants of *Dactylorchis praetermissa* in Greywell Fen, Hampshire. b, Distribution of Hybrid Index A in a sample of 50 plants from a colony of *D. fuchsii* × *D. praetermissa* at Swanscombe, Kent.

As an example of an undoubted hybrid complex, a population from near Gravesend, Kent, may be taken. In the ancient and very extensive chalk quarries in this district both *D. fuchsii* and *D. praetermissa* occur in some abundance, the latter growing often on dryish chalk, an unusual habitat for what is essentially a fen species. Hybridization between the two is frequent, and I am indebted to Dr. Francis Rose for drawing my attention to one particular complex in a quarry at Swanscombe. The floor of the excavation is covered with a dense thicket, mostly of calcicole shrubs, intersected by paths, with local copses containing ash and sycamore, some of the latter 40–50 years old. There does not appear to have been any major disturbance of the habitat during this period, although the paths are heavily enough used, and burning may be a factor preventing the development of a completely closed community. Water lies locally on the quarry floor during the winter months.

D. fuchsii mostly occurs as a component of the ground flora in the areas of scrub ; *D. praetermissa*, curiously, is mostly restricted to tracks and pathways, where many plants are greatly stunted in stature. Other dactylorchid species are scarce or absent. The hybrid complex occurs over an area of about half an acre in a region of partly cleared scrub, where during the seasons of 1952, '53 and '54 some hundreds of plants were observed in flower. The general impression gained in the field is of complete intergradation of the two parental species ; certainly the multiformity of the population suggests on first inspection that the whole forms a ' hybrid swarm '.

The distribution of the hybrid index for a random sample of fifty plants from the colony is illustrated in fig. 2 b. Three modes are apparent, about 50 per cent of the plants falling near the central mode. The remainder are mostly distributed between the two end modes, which as will be seen lie in parts of the index scale corresponding with the modes of the presumed parental species. Evidently, then, even this rough analysis is adequate to discount the superficial impression that a smoothly graded range of intermediates is present.

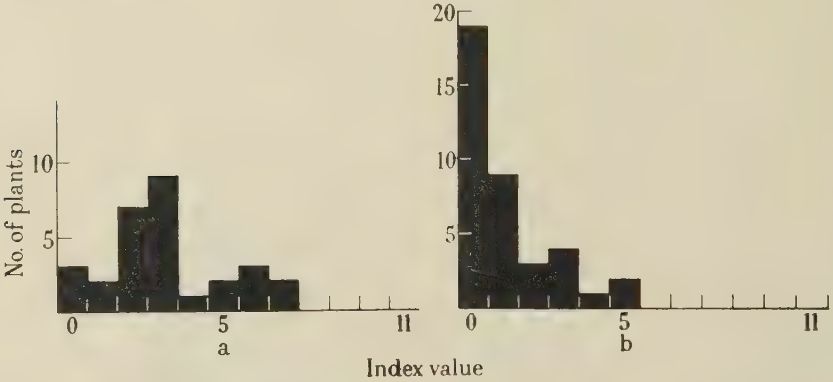

FIG. 3.—a, Distribution of Hybrid Index A, in a sample of 29 plants from a colony of *D. praetermissa* containing anomalous individuals seemingly resulting from hybridization with *D. fuchsii*, in a chalk pit near Hacklinge, Kent. b, Distribution of Hybrid Index B in a sample of 38 plants from a colony of *D. praetermissa* containing individuals referable to var. *junialis* (' *Orchis pardalina* ' Pugsl.) from water meadows near Otterbourne, Hampshire.

This is perhaps as far as the analysis of this population can profitably be taken using morphological characteristics alone, and accordingly a sample of plants was taken into cultivation in 1953 for cytological and fertility studies. The nine plants transplanted included two mainly with *D. fuchsii* tendencies, with hybrid index scores of 9 and 10 ; both proved to be diploids, with $2n=40$ chromosomes. Two mainly *D. praetermissa* with scores of 1, and one plant of *D. praetermissa* facies except for ring-spotting of the leaf, scoring 4, were tetraploids, with $2n=80$. The remainder, intermediates with scores of 5, 6, 6 and 7 were all triploids, with $2n=60$. Data concerning the seed output of two of these triploids are given in Table II.

In northern England and Wales, Scotland, and most of Ireland except parts of the west and south, the generic subsection *Majales* is represented by a complex of populations usually placed taxonomically under *D. purpurella*. Although satisfactory taxonomic subdivision of *D. purpurella* seems not to be possible as yet, three main lines of variation are apparent within it. Populations conforming with ' Form A', one of the two originally described by T. and T. A. Stephenson (1920), with a subentire, diamond shaped labellum of a bright reddish purple colour, occur in Wales, northern England and parts of eastern and northern Ireland ; outside of this area many, but not all, conform rather with ' Form B ', with a larger, more rounded and somewhat three-lobed labellum of a duller purple colour. Certain Scottish populations agree with neither of these forms and show some variation in the direction of *D. praetermissa* ; these have been named var. *pulchella*. All of these forms, and their intermediates, hybridize freely with *D. fuchsii*, and since the latter also shows geographical variation within the area of overlap, hybrid complexes of many different aspects occur.

Features in which most forms of *D. purpurella* can be differentiated from those of *D. fuchsii* with fair certainty are as follows :

D. fuchsii ($2n=40$)	*D. purpurella* ($2n=80$)
Foliage leaves 3–6 ; bract-like, 2–3.	Foliage leaves 4–5 ; bract-like, 2–3.
Lowest leaf obovate, rounded at the apex.	Lowest leaf broad, acute, keeled, recurved.
Intense leaf-marking present in 50–100 per cent of the individuals in most colonies.	Leaf-marking absent, or in the form of obscure pin-point dotting.
Labellum markedly 3-lobed ; lobes subequal. Maximum width 8–12 mm.; colour rose-pink to white, patterned with regular divergent loops, pink, purple or lilac.	Labellum rhomboidal ; typically subentire, occasionally obscurely 3-lobed ; 6–9 mm. in width. Colour intense purple, patterned with irregular bars and blotches.
Spur narrow, cylindrical ; 1–2 mm. in diam., 6–10 mm. in length.	Spur broad, bluntly conical ; 2·5–3·5 mm. in diam., 6–9 mm. in length.

Five of these differentiating characteristics fulfil the requirements for incorporation in a hybrid index, which may be composed as follows :

Hybrid Index B.

Leaf marking :	Absent	Light	Medium or heavy
Score :	0	1	2
Labellum incision :	Absent or slight	Intermediate	Deep
Score :	0	1	2
Labellum pattern :	*purpurella*-like	Intermediate	*fuchsii*-like
Score :	0	1	2
Labellum colour :	Dark reddish purple	Magenta	Pink to white
Score :	0	1	2
Spur width :	>2·8 mm.	1·9–2·7 mm.	<1·8 mm.
Score :	0	1	2

This index differs from that used above for the hybrids of *D. fuchsii* and *D. praetermissa* ; its application to populations of the former species need not, therefore, necessarily produce similar distributions. Nevertheless, different populations of *D. fuchsii* show the same degree of agreement as before (figs. 4 a and 4 b).

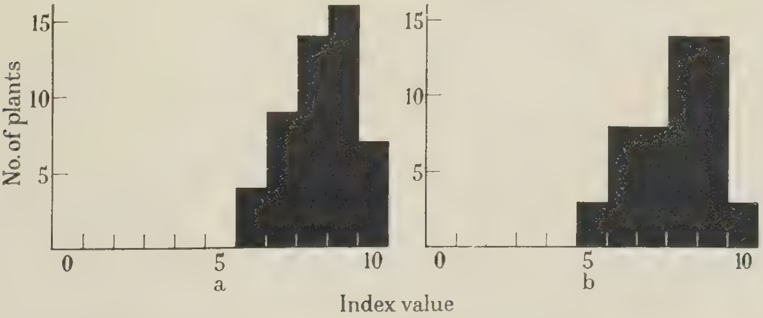

Fig. 4.—Distribution of Hybrid Index B in two populations of *Dactylorchis fuchsii*. a, 50 plants from ' tall ' chalk grassland, near Winchester, Hampshire ; b, 50 plants from ' short ' chalk grassland, near Winchester, Hampshire.

The distribution of the index in a sample of fifty plants from a population of *D. purpurella* near Conlig, Co. Down, is illustrated in fig. 5. This population is composed of plants conforming for the most part with the Stephensons'

Form A. In populations corresponding to Form B, the tendency to triple-lobing and loop-patterning of the labellum naturally shifts the mode somewhat towards *D. fuchsii*. The hybrid index is similarly affected in certain populations in the west of Ireland and Scotland where *D. purpurella* intergrades with *D. majalis* (Heslop-Harrison, 1954); these populations present problems of their own and require separate consideration.

As an example of a hybrid complex involving the two species *D. fuchsii* and *D. purpurella*, a colony near Glassan, Co. Donegal, may be taken. *D. fuchsii* is a common plant of old pastures and road verges in this district; *D. purpurella* is more local, growing mostly in marshes and poorly drained fields. A great many colonies throughout the country give the impression of being hybrid in origin, and the one analysed was selected principally because, growing as it did in an opening in a willow thicket of perhaps a quarter of an acre in extent, its limits could be established fairly easily. As in the Swanscombe colony containing hybrids of *D. fuchsii* and *D. praetermissa*, the impression produced by a first inspection of the colony was of complete intergradation between the parental species. Once again, however, the distribution of the hybrid index (fig. 6 a) suggests that three groups are present, two composed of individuals of the parental types, and the third and largest containing plants of a more or less intermediate character. Plants scoring 4 and 5 proved on cytological study to be triploid, with $2n=60$, and counts of $2n=40$ and $2n=80$ were obtained from plants from the *fuchsii* and *purpurella* ends of the distribution respectively. No other chromosome numbers were encountered.

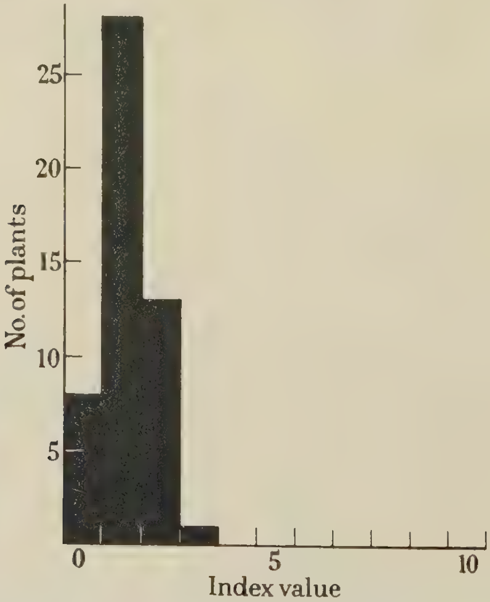

FIG. 5.—Distribution of Hybrid Index B in a population sample of fifty plants of *D. purpurella* from Conlig, Co. Down.

We see, then, that even the comparatively crude analysis provided by the use of hybrid index method suggests, both with the Swanscombe colony containing hybrids of *D. fuchsii* and *D. praetermissa* and that at Glassan with hybrids of *D. fuchsii* and *D. purpurella*, that what is actually present may be no more than a mixture of the parental species accompanied by a variable F_1. In view of the considerable intrinsic variability of the parental species themselves, segregation to the extent observed would not be unexpected, even in a single hybrid family arising from one cross-pollination. With a seed output of 2,000–3,000 per capsule, it is not inconceivable that the whole hybrid group in each instance should have arisen in this way. The uniform occurrence of the chromosome number of $2n=60$ in morphologically intermediate plants certainly does not disfavour the view that they could be first generation hybrids. Controlled pollinations carried out during the past three seasons have shown that the crosses *D. fuchsii* × *D. praetermissa* and *D. fuchsii* × *D. purpurella* each produces a full output of seed in either direction, and that, as is to be expected, the embryos are triploid.

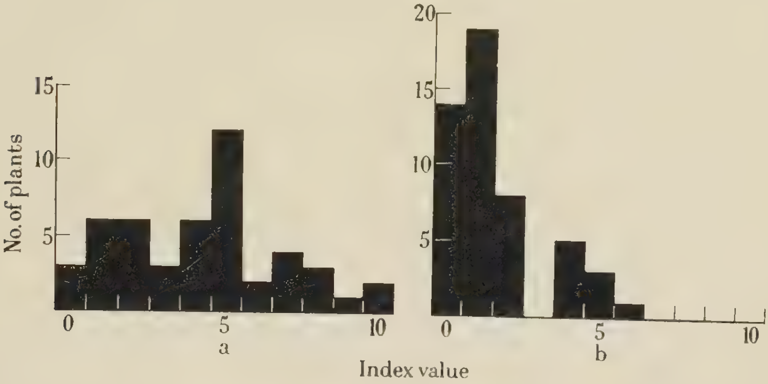

FIG. 6.—a, Distribution of Hybrid Index B in a sample of 48 plants from a colony of *D. fuchsii* × *D. purpurella* near Glassan, Co. Donegal. b, Distribution of Hybrid Index B in a sample of 50 plants from a colony of *D. purpurella* with anomalous individuals at Lough Sessiagh, Co. Donegal.

Nevertheless, this interpretation of these mixed colonies cannot be accepted without some consideration of the fertility of the hybrids themselves. There are occasional references in the literature to a supposed high fertility of hybrids between *D. fuchsii* and various marsh orchids, and the frequent assertion that colonies such as those just described are ' hybrid swarms ' carries the implication that first generation hybrids must be fertile enough at least to form back-crosses. It appears, however, that the fertility of dactylorchid hybrids has very often been judged simply on the basis of the number of swollen capsules formed, and it cannot be too strongly emphasized that this is no indication of fertility at all in any of the Ophrydeae. The swelling and maturation of the ovary to form a capsule, and even the growth and development of the ovules themselves, are a direct response to pollination, and in fact they result from the activation by the pollen tubes of a growth hormone mechanism in the ovary which can be substituted for by synthetic growth substances. In the absence of normal embryo-sacs, or of compatibility between pollen and egg, embryos are not formed, even although following pollination the ovules develop into structures simulating seeds. The simplest assessment of fertility is given by the percentage of perfect embryos formed in the seeds ; data relating to this are presented in Table II for a number of triploid hybrids of the presumed parentages *D. fuchsii* × *D. praetermissa* and *D. fuchsii* × *purpurella*. In all cases recorded in Table II, pollination has been by normal fertile pollinia from the parental species. The pollen of the triploid hybrids themselves is highly sterile (Heslop-Harrison, 1953), and selfing, while it may provoke some of the normal post-pollination effects, never results in the production of fertile seed.

The retention by the triploids of some slight fertility when pollinated from the presumed parents suggests that back-crossing may be actually possible, but in fact the situation seems to be quite different. Where chromosome counts have been possible, the embryos of fertile seeds produced by the triploids have been found to be themselves triploid, and the cytological evidence suggests that they may have been formed by the parthenogenetical development of an unreduced egg. Pollination is thus important only in so far as it provides the stimulus for ovary growth and development ; fertilisation itself does not take place.

From all the above evidence, it seems that a probable interpretation of the structure of the colonies at Swanscombe and Glassan, and presumably of others like them where hybridization of *D. fuchsii* with tetraploid marsh orchids has occurred, is that they consist of an admixture of the parents with a highly sterile, very variable first generation of triploid hybrids, possibly with a few later generation apomictic progeny of the hybrids, also triploid. There is no evidence that such colonies are ' hybrid swarms ' in the sense of Turrill, quoted above.

TABLE II.—Fertility of triploid interspecific dactylorchid hybrids judged from number of perfect embryos formed.

D. fuchsii × *D. praetermissa*			
Otterbourne, Hampshire (1953)	...	...	*c.* 1%
Swanscombe, Kent (1954)	...	...	*c.* 2·5%
Swanscombe, Kent (1954)	...	...	3–4%
D. fuchsii × *D. purpurella*			
Glassan, Co. Donegal (1949)	...	...	4%
Birtley, Co. Durham (1948, 50)	...	...	1–2%
Westport, Co. Mayo (1951)	...	...	*c.* 3%
Fenor, Co. Waterford (1951)	...	...	0%

In the two colonies just discussed, the occurrence of hybridization could hardly be in doubt whatever criterion of the process is adopted ; in each, hybrids and both parents could be distinguished both morphologically and cytologically. As pointed out by Summerhayes (1951), insect transport of pollinia occasionally takes place over considerable distances, and since a single pollination may produce some thousands of seeds, hybrid colonies become established from time to time with only one parent in the immediate vicinity. The distributions of the hybrid indices in two colonies apparently of this nature are illustrated in figs. 3 a and 6 b. In the first, a small one in a chalk pit near Hacklinge, Kent, the ' pure ' species present is *D. praetermissa*, in the squat form characteristic of dry habitats ; plants of this group proved to be tetraploid and fully fertile. The remainder of the colony consisted in 1952 of a variable group of individuals, clearly, as may be seen from the distribution of the hybrid index, bearing the marks of hybridization with *D. fuchsii*, which was not itself seen within three hundred yards of the colony. Three plants from this element all proved to be triploid. The second exemplifies a parallel situation with *D. purpurella*. This colony, growing in tall sedge meadow at the south end of Lough Sessiagh, Co. Donegal, while principally composed of *D. purpurella*, contained in 1949 several individuals strikingly like the hybrids in the Glassan population described above. All of those examined cytologically proved to be triploid and practically entirely sterile. The nearest plants of *D. fuchsii* occurred at the north end of the lough, some $\frac{1}{4}$ m. distant.

Although it was not my intention to deal here in any detail with the problems presented by the internal variability of tetraploid marsh orchids themselves, I feel I must conclude with a mention of the question of Pugsley's '*Orchis pardalina*'. As we have seen, the original diagnosis of *Dactylorchis praetermissa* was based upon plants without leaf spotting. However, nearly all populations contain a proportion of plants in which anthocyanin leaf-marking, usually in the form of rings, is present. Two rather distinctive floral features are correlated with leaf pigmentation in these plants. One is the appearance of labellum patterning in the form of continuous double loops, in contrast with the patterning of fine dots characteristic of the type form; the other is a tendency for the prolongation of the central lobe of the labellum. These features have gained taxonomic recognition for this element in *D. praetermissa* populations; firstly under the ambiguous name '*Orchis latifolia*' (e.g., Godfrey, T. A. & T. Stephenson, 1924), and more recently under the varietal name *D. praetermissa* var. *junialis* (Vermeulen, 1933) and the specific name *Orchis pardalina* (Pugsley, 1935). The character in which var. *junialis* departs from typical *D. praetermissa* may be interpreted as a shift from the norm of the species towards the generic subsection *Eumaculatae*, in particular, perhaps, towards *D. fuchsii*.

Because of this, several authors (including Druce, 1923, and Clapham, 1952) have suggested that all such plants are, in fact, of recent hybrid origin. In the hybrid index as compounded above leaf marking and labellum lobing are incorporated so that its distribution is affected in populations containing an appreciable proportion of plants with the facies of var. *junialis*; an example is given in fig. 3 b. However, this merely serves to illustrate the pitfalls attending the use of simplified methods of analysis like the hybrid index. The polarized variation apparent in this Otterbourne population may suggest the influence of hybridization, but plants scoring 5 are tetraploid and fully fertile, this being the element referable to var. *junialis*. Furthermore, in spite of their correspondence in some of the characteristics incorporated in the hybrid index, plants of var. *junialis* are far from being identical morphologically with the triploid hybrid, *D. fuchsii* × *D. praetermissa* (Pugsley, 1935). *D. praetermissa* is itself probably an allopolyploid and thus a product of hybridization (Heslop-Harrison, 1953); it is no doubt in this origin that we have to seek the cause of the genetical instability which results in the segregation of plants of the *junialis* facies. Certainly they do not appear to be the products of recent hbyridization between *D. praetermissa* and *D. fuchsii*.

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